POPULATION MODEL FOR ALASKA PENINSULA
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Population Model for Alaska Peninsula Sea Otters

Population Status of California Sea Otters
Pacific OCS Region
Minerals Management Service
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OCS STUDY
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POPULATION MODEL
FOR
ALASKA PENINSULA SEA OTTERS

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS....................v

LIST OF FIGURES AND TABLES....................vi

ABSTRACT....................ix

1.0 INTRODUCTION....................1

2.0 INFORMATION ON N. ALEUTIAN BASIN SEA OTTERS....................3

2.1 The 1976 census....................3
2.2 More recent censuses....................4
2.3 Current biological studies....................5
2.4 The effect of severe winter weather....................6

3.0 DATA FOR PARAMETER ESTIMATION....................7

3.1 Data from experimental harvests in the Aleutians....................7
3.2 Sea otter population trends....................8
3.3 Distributional patterns....................11

4.0 OIL SPILL EFFECTS....................16

4.1 Effects of oil on sea otters....................16
4.2 Incursions of sea ice....................17

5.0 CONCEPTUAL POPULATION MODELS....................18

5.1 The California model....................18
5.2 Circumstances in the Bering Sea area....................20
5.3 The conceptual approach....................20

6.0 ASSUMPTIONS AND INITIAL CONDITIONS....................22

6.1 General procedure for developing assumptions....................22
6.2 Parameter estimates needed....................23

7.0 SURVIVAL ESTIMATES....................25

7.1 Survival estimates from age structure data....................25
7.2 Aleutian age structure data....................25

7.3 California age structure data 29
7.4 Estimate of early survival rates 34
7.5 Stationarity and age structure data 34
7.6 Pup survival rates 35

8.0 REPRODUCTIVE RATES 38

8.1 Reproductive cycle 38
8.2 Pregnancy data 40
8.3 Observations on pupping cycle -- Alaska 40
8.4 Observations on pupping cycle -- California 42
8.5 Interval between births 43

9.0 POPULATION MODEL 48

9.1 Mathematical structure of the population model 48
9.2 Computer formats for population model 48
9.3 Parameter estimates for the model 49
9.4 Versions of the model 51
9.5 Basic model 52
9.6 A projection model 52
9.7 A model with two sexes 52
9.8 Population model with density dependence 54

10.0 PARAMETER ASSESSMENT AND DATA NEEDED 57

10.1 The bootstrap approach to assessing data sets 57
10.2 Bootstrapping the telemetry data 57
10.3 Increasing sample sizes for calculations 58
10.4 An alternative estimate of early survival 62
10.5 Population growth rates for Alaskan sea otters 63
10.6 Parameters for high population growth rates 67
10.7 Likely parameter values for Alaska Peninsula population 67

11.0 APPENDIX 69

11.1 IBM-Compatible version of main models 69
11.2 Formulas for MULTIPLAN MODELS 71
11.3 BASIC program corresponding to MULTIPLAN model 75
11.4 BASIC program used to fit survivorship function 78
11.5 BASIC program used to fit survivorship function(Calif.) 79
11.6 BASIC program (ALEUT2) used to produce data for Fig. 7.6 79
11.7 BASIC programs used to produce data for reproductive cycles. 79
11.8 Bootstrap programs 80
11.9 Outputs from MULTIPLAN spreadsheet models 87

12.0 LITERATURE CITED 93

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LIST OF FIGURES AND TABLES

Fig. 1.1 General map of area and major place names 2

Fig. 2.1 Aerial counts of sea otters -- Unimak Island 3

Fig. 3.1 Population estimates --Amchitka Island 9

Fig. 3.2 Recorded extent of sea otter population range 10

Fig. 3.3 Comparison of sea otter counts in August and October of 1982 12

Fig. 3.4 Sea otter counts in August and October,1982 with Transect 24 deleted 12

Fig. 3.5 Sea otter counts in August, 1982 and March 1983 13

Fig. 3.6 Comparison of 1982 and 1976 counts with Transect 24 deleted 13

Fig. 3.7 Comparison of counts in August and October of 1982 14

Fig. 3.8 Comparison of 1976 and August 1982 counts 15

Fig. 3.9 Comparison of 1976 count and August 1982 15

Fig. 5.1 Flow diagram for sea otter population model 19

Fig. 5.2 Conceptual approach for modelling study 21

Fig. 6.1. Locations of concentrations of sea otters 23

Fig. 7.1. Ages of western Aleutian female sea otters 25

Fig. 7.2. Constant survival rate for female sea otters 26

Fig. 7.3. Fit of a survivorship curve to ages of female otters 27

Fig. 7.4 Expected values for a constant survival rate 27

Fig. 7.5. Senescence curves 28

Fig. 7.6. Survivorship curve for female Aleutian sea otters 28

Fig. 7.7 Ages of sea otters found dead 29

Fig. 7.8. Constant survival by Chapman-Robson method 31

Fig. 7.9. Survivorship curve for female California sea otters 32

Fig. 7.10. Expected distribution at age of death 32

Fig. 7.11. Expected distribution with changed parameters 33

Fig. 7.12 Fit of Chapman-Robson survival estimate to ages at death 33

Fig. 7.13. Index counts of selected California areas....35
Fig. 7.14. Index counts of California sea otter range, 1982-1985....35
Fig. 7.15. Relative numbers of small and large pups....36
Fig. 7.16 Relative numbers of "large" pups....37
Fig. 8.1. Apparent pupping cycle of Alaskan sea otters....39
Fig. 8.2 Assumed cycles of pregnancy and pupping....39
Fig. 8.3 Observed pregnancy rates in a sample of sea otters....40
Fig. 8.4 Pups per independent otter -- Prince William Sound....41
Fig. 8.5 Data on pups per independent otter -- Amchitka Island....41
Fig. 8.6. Pups per independent--Amchitka Island,1987....42
Fig. 8.7. Small pups per independent otter -- California....43
Fig. 8.8. All pups per independent otter....43
Fig. 8.9 Basis for estimating duration of reproductive cycle....44
Fig. 8.10. Estimated length of reproductive cycle....45
Fig. 8.11. Plot of difference between estimates....46
Fig. 8.12. Pup dependency intervals....46
Fig. 9.1 Reproductive and survivorship curves....51
Fig. 9.2. Components of the population models....51
Fig. 9.3 Stable age distributions for male and female otters....53
Fig. 9.4 Variation in density-dependence function....54
Fig. 9.5 Population trend after a simulated oil spill....56
Fig. 10.1 Frequency distribution of 300 values of lambda....58
Fig. 10.2. Age distribution of female otters found dead....59
Fig. 10.3 Survival estimates from telemetry data....60
Fig. 10.4. Reproductive rates from small sample....61
Fig. 10.5. Estimates of lambda....62

Fig. 10.6. Estimates of lambda using proportion of "immatures" 63

Fig. 10.7 Locations of sea otter transplants 65

Fig. 10.8. Regression lines for area north of Sitka 66

Fig. 10.9. Regressions in the Maurelle and Barrier Islands areas 67

Table 11.1 Example of output for basic population model 87

Table 11.2 Projection model with two sexes (OTTERS2) 88

Table 11.3 Population model with A = 0.30 89

Table 11.4 Projection model with density dependence 90

Table 11.5 Final projection model (OTTERS4) 91

ABSTRACT

The present study was conducted to provide a basis for assessing risks of oil spills to sea otter populations along the Alaska Peninsula. The principal efforts were devoted to analyzing the available data on population dynamics. Curves characterizing survivorship and reproduction for sea otters were devised and fitted to several data sets. A detailed review was conducted of methods of assessing population dynamics data, and several new techniques (e.g., bootstrapping) were applied to available data. A simplified model for use with Alaska Peninsula sea otter populations was devised and implemented in a "spreadsheet" format. Various aspects of model development and data on population size in Alaska Peninsula areas were reviewed.

1.0 INTRODUCTION

This report was written to fulfill the requirements of a modification of contract No. 14-12-0001-30033 (Population status of California sea otters) with the University of Minnesota, titled "Quantification of expected population response of Alaska Peninsula sea otters to hypothetical oil spills". The study was funded by the Minerals Management Service to enhance information and techniques for the assessment of potential effects of offshore oil and gas activities on sea otters inhabiting offshore areas adjacent to the Alaska Peninsula.

By way of a general introduction to the report, we note that it is unrealistic to attempt to use the existing model for the California population for otters along the Alaskan Peninsula due to the lack of certain detailed information about Alaskan populations. Further discussion of these points is provided in the appropriate places below. Two approaches were developed to meet the needs of the Minerals Management Service. The first was to develop statistical and computer methods to combine various sources of population data for parameter estimation. We also evaluated the various available Alaskan data sets, in particular those collected by the Alaska Department of Fish and Game some years ago, along with the results of our work in Prince William Sound, and various other data sets. The major technical problem is that very different sets of data are to be combined. One source includes indirect estimates of parameters, such as survival rates, that are based on sources such as the ratios of young pups to "independent" otters contrasted to ratios of older pups to independent otters. The other major source is direct estimates of survival made with telemetry on quite small samples. Pregnancy rates may also be observed on the telemetered otters, while some pregnancy rates were obtained in Alaska from samples of harvested otters.

Where independent sources of the same parameter (such as survival) are available, the different estimates might be combined by inverse weighting by variance estimates. However, the various telemetry estimates (survival, pregnancy, etc.) are not from independent samples, being based on the same set of female otters, and the rates inferred by indirect means may also require the assumption of some basic parameter, such as survival of female otters. Consequently, a fairly complex analytical effort was needed involving extensive computer calculations.

Our second approach was devoted to development of a modified population model, appropriate to Aleutian conditions and data. It seems likely that an interactive computer model using maps of the site might also be useful in discussing effective deployment of cleanup equipment and introduction of other mitigative measures. Major locations referred to in the study are shown in Fig. 2.1.

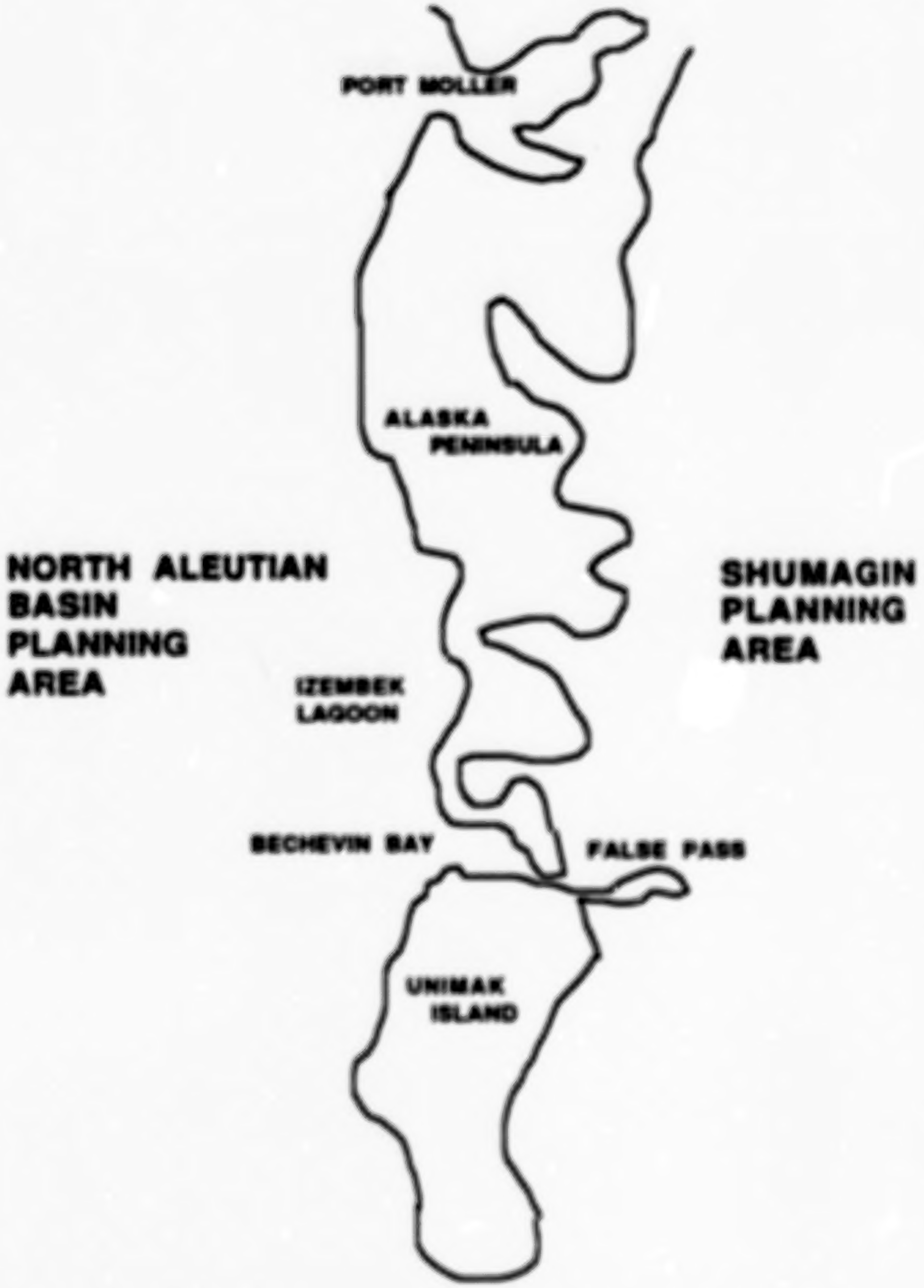


Fig. 1.1 General map of area and major place names referred to in this report.

2.0 INFORMATION ON N. ALEUTIAN BASIN SEA OTTERS

Unfortunately, the current state of biological information on sea otters in the area is limited, and is unlikely to be adequate to support much complexity in modeling. As pointed out in the proposal and in response to comments, the California model had to be substantially revised to make it useful with the available information. Further details of the needed revisions will be given in succeeding sections of this report. Here we discuss the available census data and some data on movements and biological attributes of the population.

2.1 The 1976 census

The available data on population size and distribution of sea otters in the area north of Unimak Island and the Alaska Peninsula are based largely on a census method designed by Schneider (1976). A systematic aerial strip transect census of sea otters was conducted north of Unimak Island and the Alaska Peninsula. The census covered an area reaching from nearly the western end of Unimak Island to the vicinity of Port Moller, and was conducted on 30 and 31 July, 1976.

Schneider (1976) noted that the population in this region is unique in that it ranges widely in shallow offshore waters, whereas most sea otter populations reside close to shore, concentrating in areas with offshore rocks and kelp beds. At times, the population appears to be concentrated within a few kilometers of the adjacent sandy beaches, but frequently scatters to the vicinity of the 80 m depth contour, 50 km or more from shore.

A number of fixed wing aerial surveys were flown in years prior to the 1976 survey, starting in 1957. None of these prior counts systematically covered the entire area, and numbers of otters counted varied greatly, presumably due to weather conditions and season of count. Counts of the principal concentration area (north of Unimak Island and the eastern end of the Alaska Peninsula) are of particular interest since they suggest a long-term occupancy by substantial numbers of otters (Fig. 1.1). A remnant population is believed to have survived the period of commercial exploitation prior to 1911, and to have been concentrated in this region.

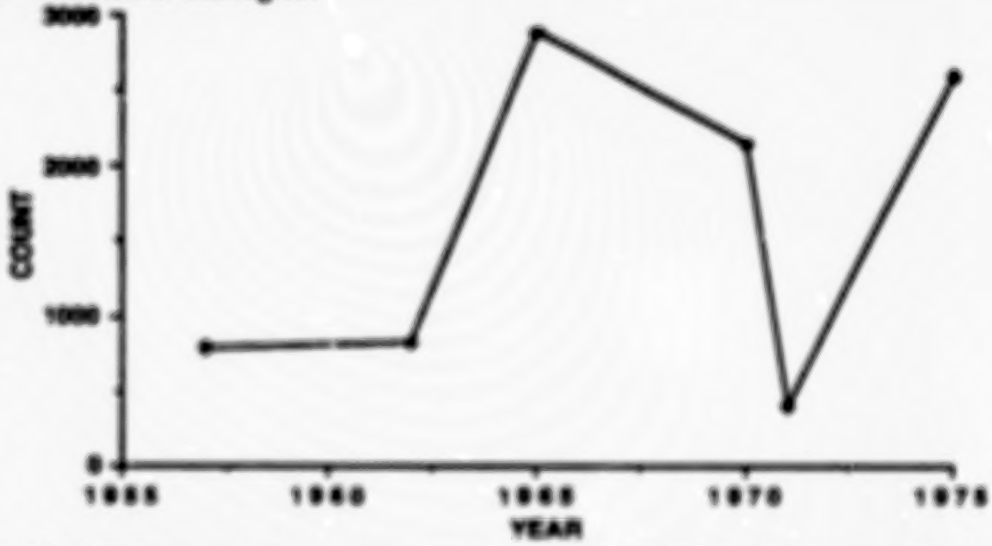


Fig. 2.1 Aerial counts of sea otters in the area north of Unimak Island and the western Alaskan Peninsula, made prior to the systematic aerial census of 1976. These counts were made under varying circumstances, and none were intended as a full-scale census of the otter population, as made in 1976.

Presumably the 1970 population in the study area exceeded the numbers estimated to be present in 1976, since Schneider (1976) reported that sea otters were commonly seen in the earlier years well beyond Port Moller, as far as Port Heiden, with occasional individuals observed deep into Bristol Bay. In 1971, 1972, and 1974 sea ice, which normally forms only to the vicinity of Port Heiden, advanced to Unimak Island. These excursions, discussed below in more detail, appeared to restrict the range of the population and may well have reduced numbers present.

The 1976 survey was conducted along systematically spaced north-south tracklines extending from shore to the vicinity of the 90 m depth contour over much of the major occupied range. The survey was conducted from the turbo Goose N780 operated by the U.S.Department of the Interior, at an altitude of 200 ft. and airspeed of 120 knots. Two observers counted all sea otters seen within 0.1 nautical mile wide strips on either side of the aircraft. Two other observers sat in the rear of the aircraft and recorded all sea otters seen, regardless of distance from the aircraft. Visibility conditions were tallied throughout the survey, and evidently were remarkably good in terms of conditions normally encountered in the region. Detailed results are available for the survey, in 2 nautical mile long segments along with time of day, prevailing visibility conditions, activity status of otters, and group size. A total of 1901 sea otters were counted in the unlimited transects while 811 were tallied in the 0.2 nm transects. Major uncertainties included the effect of animals that were submerged when the aircraft passed over, and the possibility of missing some surfaced otters in the transect areas. Three transects (Nos. 36-38) were not surveyed due to fog.

Total population size was estimated on the basis of an overall area of 7175 km2 within which 506.3 km2 were actually counted for a total of 811 otters. A few small corrections for counting conditions and otters tallied in Bechevin Bay were added to give an estimate of 12,021 otters on the surface. A correction of 30 percent for submerged otters then yielded an overall estimate of 17,173 sea otters in the area.

An important feature of Schneider's (1976) report is his observation that "this population is more mobile than those occupying typical, rocky, sea otter habitat. Differences generally have been in degree of dispersal offshore. At times large numbers have been concentrated near shore while at other times low densities occurred 15 to 30 km from shore. The 30-31 July 1976 distribution appears intermediate between these extremes and may be more typical. There appeared to be at least two separate areas of high density roughly separated by a line between Amak Island and Cold Bay. This separation has been observed on past surveys and may reflect varying quality of habitat." He also noted that weather seems to play a role in determining distribution offshore, with concentrations near shore following severe storms while the otters tend to be further offshore and widely dispersed after several days of calm weather.

2.2 More recent censuses

More recent counts of otters in the same area were reported by Cimberg and Costa (1985). Those authors repeated the transects flown by Schneider in June 1982, August 1982, October 1982, and March 1983. The same strip width was used, "at an altitude of 150 to 200 ft. at approximately 120 mi." Poor weather in June precluded the sampling of all transects, so that survey is not considered further here (a total of only 46 otters was recorded). Population estimates of 10,325 for August of 1982, 4,737 in October of 1982, and 1,454 in March of 1983 were reported.

These results led the authors to suggest that "these results indicate two seasons, with a summer period of high abundance (July, August, or September) with over seven times as many otters present as during the winter (October to June))." They also stated that "the largest net influx of otters into the area occurred between June and August, particularly in the Unimak, Izembek and Port Moller areas", and that "Migration likely occurred from Bechevin Bay via False Pass from populations in the Pacific since this proposed route is shallow, allowing periodic feeding as is apparently necessary. Highest sea otter concentration was seen in the Bechevin Bay - Izembek Lagoon area where the otters would first enter the Bering Sea." A further statement was made that "results from this study indicate that sea otters migrate from the Pacific Ocean, where they feed (on urchins and molluscs ?) in the winter, to the Bering Sea in the summer, where they feed on fish, crabs, and clams." No additional evidence of such a postulated migration has been obtained in subsequent studies.

Bruggeman (1987) reported surveys conducted between March amd April, 1986, using a DeHavilland Twin Otter aircraft. Three types of surveys were flown. Systematic surveys were essentially the transects described above, flown at 90m and 100 knots air speed. Coastal surveys covered near-shore areas missed in the systematic surveys, while island surveys consisted of flying the perimeter of islands. Effort was allocated as 51% to the North Aleutian Planning Area, 45% to the Shumagin Planning Area, and 4% to the St. George Planning Area (Fox Islands).

Sea otter population size estimates for the N. Aleutian area were 13,091 for the summer period, and 9,061 for the fall (Bruggeman 1987:Tables 11-13). The Shumagin Planning Area estimates were 17,835 in spring, 15,346 in summer, and 16,856 in the fall. The St. George area population was reported as 858 otters.

2.3 Current biological studies

Further recent work in the study area has been summarized by Monnett and Rotterman (1986). They noted that the recent estimates suggest that the current population may be below that present during the 1976 survey and suggested that a density-dependent mechanism may be responsible, by way of a population increase beyond carrying-capacity in the 1970's and a subsequent decline, presumably due to reduced food supply. An alternative density-independent mechanism was suggested as possibly being due to periodic episodes of ice incursion into the area. It was proposed that a choice between the two hypotheses might be based on physical condition of individuals, reproductive rates, and pup survival rates.

Sea otters were captured in Bechevin Bay and on the S.E. side of Amak Island in July and August of 1986, using floating tangle nets and dip nets (for dependent pups). Weights and total body lengths were taken, and red, numbered plastic tags were affixed to a hind flipper. Sixteen otters (12 female and 4 males) were equipped with implanted radio transmitters, while 22 dependent pups were tagged. Aircraft were used to search for the instrumented otters on 4 occasions in August and 4 in October. Movements appeared to be closely comparable to those observed in California and in Prince William Sound. One otter moved south through False Pass into the Pacific. The overall impression from the study reinforces the suggestion of Schneider, discussed above, that sea otters move freely back and forth from Bechevin Bay out into the Bering Sea. During late July, one thousand or more otters were concentrated in the vicinity of Bechevin Bay. "It was determined that these were almost all females during capture activities. By August 7, there were only a few hundred individuals remaining in that area." Also, " after many of the individuals had left Bechevin Bay, several large female concentrations had formed in the Bering Sea." It was remarked that "the behavior of the Bering Sea population appears not to differ substantially from that of other populations which move periodically between open and more protected waters, such as the Orca Inlet - Copper River Delta and California populations, except in that some individuals may move greater distances offshore."

A preliminary assessment of physical condition indicated that "the Alaska Peninsula females were in as good or better condition than the Prince William Sound females." Several of the Alaska Peninsula females were among the heaviest ever recorded. Similar results were suggested for adult males. Also, "the Alaska Peninsula pups were fatter than the pups at the other locations" (Green Island in Prince William Sound and Amchitka Island). It was concluded that "this data set suggests that the hypothesis that the Alaska Peninsula population has exceeded habitat carrying-capacity should be rejected."

2.4 The effect of severe winter weather

A very important element of background information on the Alaska Peninsula otters is the potential for incursions of sea ice into the occupied area. A good description of such effects was reported by Schneider and Faro (1975). Two incursions were studied (1971 and 1972). Subnormal temperatures were reported along most of the Alaskan Peninsula in January of 1971, and the ice pack had advanced to Port Moller by the end of the month. The pack retreated in February, but advanced again with lower temperatures with all-time record low temperatures on 12 and 13 March, with considerable ice reaching Unimak Island and covering much of the sea otter habitat in the area. In aerial surveys on 10 and 12 March 1971, a number of dead otters and tracks of otters on shore were observed. By 15 March the main pack edge had reached south of Amak Island, but was then pushed north by warmer temperatures and southerly winds.

The 1972 incursion was more extensive, reaching Unimak Island by 12 March, with substantial amounts of ice reported near Unimak Pass. Aerial surveys were conducted on 3 March and 15 March, 1972. Residents of Cold Bay reported numerous sea otters seen on the ice, with 127 sets of tracks leading from the Bering Sea counted along 5 km of beach, and 34 otters captured and moved to the Pacific side. The 15 March aerial survey results indicated that several thousand otters were occupying the area immediately north of Izembek Lagoon, Bechevin Bay and Unimak Island. Hundreds of sets of tracks were observed on sea ice, indicating substantial movements between leads of open water, but no recent tracks were observed on shore. By 27 March, warming conditions resulted in a retreat of the pack ice to Port Moller. Low temperatures caused another incursion to the Izembek area by 13 April. Seven apparently healthy otters were observed near holes in extremely heavy ice north of Port Moller on 14 April. Another formation of ice to the Izembek area occurred again between 24 and 26 April.

The overall impression of the authors was that the otters seen ashore were trapped as ice froze around them, particularly in 1971. However, it appeared likely that most otters moved ahead of the ice. The available records suggested that a minimum of 200 otters died in 1971, but an upper limit could not be ascertained. Otters did not appear to be seriously affected by sea ice until perhaps as much as 90 percent or more of the surface was ice-covered. Starvation, rather than low temperatures, was implicated as cause of death. Few young pups were observed, and it seemed likely that subadults suffered the most severe mortality. However, many of the dead animals retrieved on land in 1971 were adults. It was stated that, "Although we were unable to accurately assess mortality in either year, it appears that most of the animals in the population survived."

3.0 DATA FOR PARAMETER ESTIMATION

Relevant biological data on the population of immediate concern is limited in scope, and was reviewed in the preceeding section of this report. As noted in the Introduction, much of our efforts in the study have had to be devoted to attempting to derive useful parameter estimates from other sources of data on sea otters. Some of these sources are described in this section.

3.1 Data from experimental harvests in the Aleutians

The most extensive data on reproduction for areas near the study site are those collected in an experimental harvest program in locations further west in the Aleutian chain. Nearly 1500 female reproductive tracts were collected between 1967 and 1971 from sites around Adak, Kanaga, Tanaga, and the Delarof Islands and Amchitka Island in the central and western Aleutians. Results were reported by K.B. Schneider (Schneider, unpublished). Most of the specimens were from animals shot during experimental harvests, but 135 were from females that died during transplanting operations. Two important potential sources of bias need to be considered. One is the fact that otters may give birth over much of the year. Hence, the data had to be analyzed on a monthly basis. The other problem is that hunters were reluctant to shoot females with pups during a harvest. Only one sample of 50 females collected 24-28 June, 1971 on Amchitka Island was collected "as randomly as possible."

Mating activity in Aleutian otters occurs throughout the year and reaches a peak in September and October. A period of increased birth rate appeared to begin sometime in April, reached a peak in May, and was over by mid-June. The period between the peak of mating activity, about October 1, and the peak of pupping, May 15, is about 7.5 months, which should thus roughly equal the gestation period, according to Schneider's (Schneider, unpublished) report.

A fetal growth rate curve was developed and used to estimate the birth dates for fetuses, which were in turn expressed as potential births per 100 sexually mature females. This yielded an annual birth rate of about 55 births per 100 sexually mature females (data were adjusted on the assumption that hunters had avoided 15 percent of the sexually mature females because they were accompanied by pups). It was suggested that a relatively high percentage of females with pups begin an estrus cycle but that there is a high rate of failure to complete the cycle. However, it was also stated that "Some females appear to have formed an average of one corpus albicans per year and most formed more than one every two years after reaching sexual maturity. This would tend to indicate a shorter interval between pregnancies..." (shorter than the then generally accepted mode of one pup every two years).

The conclusion of this study was summarized as "it appears that most females mate in fall, give birth the following spring, and rear their pup for about a year before becoming pregnant again even though they probably entered estrus at least once during that year. Since there is a distinct annual rhythm of sexual activity in the population, most females probably become pregnant the following fall, completing the cycle in 2 years." The age of sexual maturity was described by "Most females appeared to become sexually mature when between 3 and 4 years old... No females less than 3 years old were mature and all but one 4 year old were mature." Also, it was indicated that most females "probably bear their first pup... near their fourth birthday."

There did not appear to be a definite maximum breeding age. One of the oldest females collected (23 years old) had a pup and other old females were pregnant. Twenty percent of females over 17 years old (collected in fall, 1968) were pregnant while 41 percent of all sexually mature females were pregnant. However, 54 percent of females over 15 years old collected in May, 1970 were pregnant compared to 59 percent of all mature females. It was noted that "While the pregnancy rate of older females may or may not be lower, they appear to have a high incidence of failure of pregnancy. Of 11 females between the ages of 18 and 21 years, collected in May, 1970, four were resorbing blastocysts or fetuses and only three were supporting normal pregnancies."

An important point was made that "High rates of in utero mortality may be associated with poor nutrition. Sea otters in the area of highest mortality at Tanaga Island appeared in poorer physical condition and were smaller than those in other areas." It was also stated that "Tanaga sea otters were in poorer physical condition than those at Amchitka. Otters at Adak Island were in better condition than those at any of the other islands."

3.2 Sea otter population trends

An essential feature of modeling oil spill effects is the development of estimates of potential rates of growth of otter populations in the affected areas. At present, relatively little information of this kind is available for the primary sites, and it has not been feasible to examine data from other, comparable sites in much detail. Some earlier reports suggest rather high rates of growth for Alaskan otters, but these need to be examined in more detail. Sec. 10.5 describes rates observed recently in Southeast Alaska.

Although the expansion of range and thus probably an overall increase in total numbers continues in Alaska, there is an important issue in terms of condition of populations that have long since reached peak abundance. The only extensive set of population data is that for Amchitka Island. Kenyon (1969:Table 23) gave counts and estimates from 1936 to 1965, and Estes (1977:Table 5) provided counts from 1968 to 1972. The data provided by Kenyon were based on both surface counts and those from fixed-wing aircraft. Various corrections were used to attempt total estimates. The more recent counts were made from helicopters. A plot (Fig. 3.1) of the earlier estimates and the recent helicopter counts gives an impression of the course of the population on Amchitka. A much higher estimate for 1956 was given by Lensink (1962:60), who estimated the total population to be 5,637 otters in that year. Neither Kenyon (ibid:156) nor Estes (ibid:523) were willing to accept that estimate. Using a combination of aerial counts and shore-based counts of limited areas (for adjustments), Estes (ibid:521) estimated the total population in the 1970 period as 6,432 sea otters.

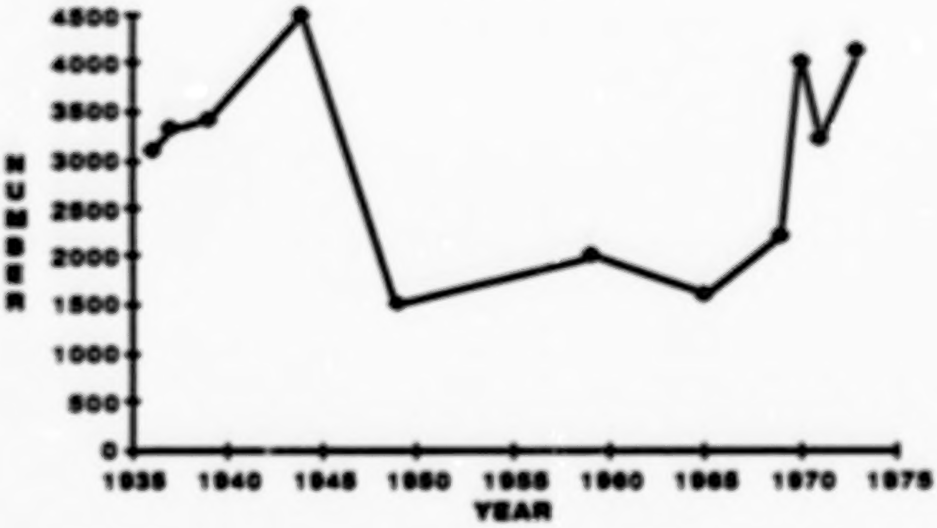


Fig. 3.1 Population estimates and counts of sea otters on Amchitka Island, Alaska.

A general impression from the counts and estimates is that the Amchitka population peaked in the 1940's, declined in the 1950's and 1960's, and may possibly have subsequently increased in the late 1960's. The earlier observations showed that the bulk of the population was on the Pacific (south) side of the island and later expanded along the Bering Sea side. In the period of population decline there were winter die-offs from starvation (Kenyon, ibid:250-267). On the basis of shoreline counts of carcasses, Kenyon (ibid:267) estimated an annual mortality in the seasons of 1959 and 1962 on the order of 10 percent. There is thus some evidence that the Amchitka population over-utilized its resources by the late 1940's, declined sharply and remained at a lower level for some 20 years. Whether or not the population may then have recovered to higher numbers depends on how one reconciles the two types of counts and the estimation methodology used by different authors.

Population estimates for California in the mid-1970's were on the order of 1700 to 1800 sea otters (California Department of Fish and Game, 1976). These estimates were, in effect, projected back in time by using data on the coastal area occupied by sea otters since 1933. This was calculated from an assumed maximum effective foraging depth for the California population. A somewhat higher density of otters was assumed in the earlier years (roughly 14 per square mile) as contrasted with more recent years (12 per square mile). The result is an estimate of about 300 sea otters in 1933, which is in reasonable accord with observations in the early years.

The resulting data suggests a rate of increase of about 5 percent per year (CDFG, ibid). An alternative approach is to examine the range expansion data directly. Using non-linear least squares fits to an exponential growth model, the data on linear miles of coastline occupied gave:

$$y = 9.71e^{0.044x}$$

where y = linear miles of coastline occupied, and x denotes time in years since 1933. The main departure from exponentiality appears to be in the late 1960's, and may be associated with the otter "invasion" of Monterey Bay.

A fit to estimated square miles of habitat occupied gives the model:

$$y = 5.18e^{0.053x}$$

where y now denotes square miles occupied, and x is time from 1933, as before. In this case, the deviation in the late 1960's is not so apparent, but the last (1979) point is appreciably above the trend line. A possible factor here is the subsequent expansion over a long stretch of sand beach to the north of Monterey Bay. The data used for the two fits are those of the CDFG as modified by Benz and Kobetich (1980), with the exception that the area for 1979 was calculated by multiplying the linear mileage by 1.1, a factor determined from the last area calculation reported (1975).

The annual rate of expansion by area (0.053) is about that reported for population growth (CDFG, ibid), while the linear rate (0.044) is somewhat smaller. In both cases, the data suggest a continued expansion at an exponential rate. Whether or not the population numbers continued to increase along with the range depends of course on densities within the range. More recent data indicates that expansion of numbers may well have stopped about 1976. Figure 3.2 shows the expansion data up to recent years.

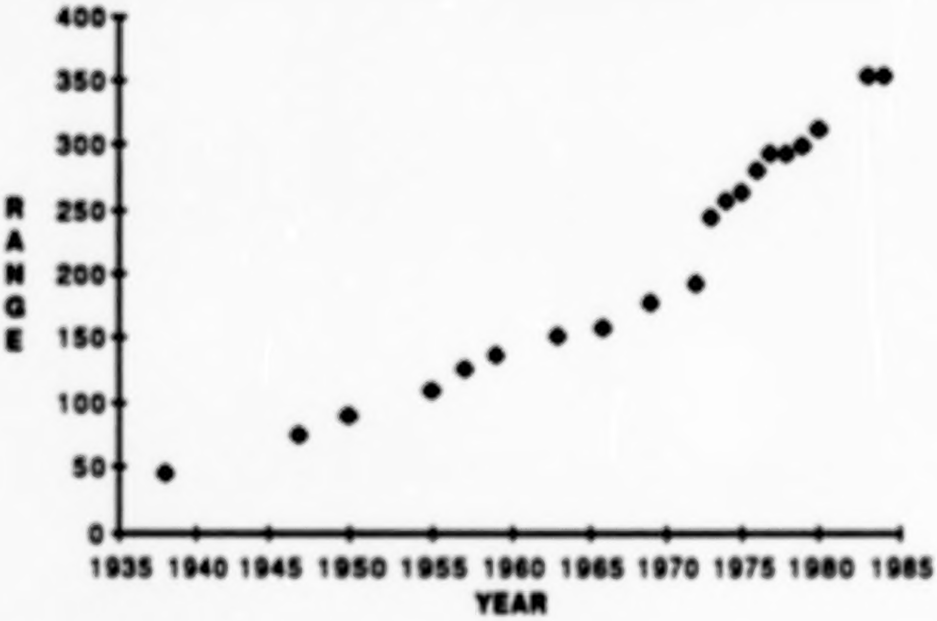


Fig. 3.2 Recorded extent of sea otter population range (km).

An intriguing question about the California population is whether or not the apparent rate of growth is a function of the entire population. That is, two models for expansion might be postulated. One would involve the movement of "surplus" individuals from throughout the range to the expansion "fronts". Another might be based on equilibrium conditions in some central part of the range, with vigorously growing subpopulations closer to the "fronts".

Various sources (CDFG, ibid; Benz and Kobetich, ibid) have suggested that the California population has shown appreciably lower rates of growth than have those in Alaska. Such an assertion would seem to depend on the assumption of the first model suggested above, i.e., that the entire population contributes to the growth measured by range expansion. A further difficulty is that the estimates of growth of the Alaskan population are necessarily based on counts of segments of that population, made by different people using various methodologies (shoreline counts, vessel counts, several types of aircraft). There is thus a lack of consistent sets of data from which to calculate a rate of increase. An additional problem is that the apparent rates of increase at one island may include an influx of immigrants from nearby islands with peak populations.

Lensink (ibid:108) justified rates of increase of 10-15 percent per year on the basis of back-calculations. He cited Russian observations of 5-7 percent rates of increase on the Commander Islands, but argued that these rates would require larger initial populations than seemed likely to be present at the end of the exploitation period (about 1911). The higher rates gave initial populations that he believed to be more realistic.

A very important component of data needed to model potential oil spill impacts on sea otters will be the spatial distribution of the population. Actual field data available when the present analyses were conducted were limited to four transect counts on the Bering Sea side of the study area. These included the original observations made by Karl Schneider in 1976 and 3 transects surveyed by Cimberg and Costa (ibid), in August and October of 1982, and in March of 1983. These surveys were discussed above, along with some subsequent investigations reported by Bruggeman (1987).

3.3 Distributional patterns

Use of the Bering Sea transect data may be evaluated by considering correlations between the various counts. The main information on recent distribution comes from the count in August of 1982 (529 otters tallied), with supplementary data from a count in October of 1982 (234 otters counted), and very limited data from the count of March, 1983 (only 73 otters were recorded). More than 40 percent of the individuals seen in the August, 1982 count were concentrated in transect No. 24 (226 of the total count of 529 otters) As is evident in Fig. 3.3 , this high single count makes it difficult to examine correlations between the different counts.Hence Figs. 3.4 and 3.5 show comparisons of the recent counts without Transect No. 24. Fig. 3.6 shows a comparison of the highest recent counts (August of 1982) with the 1976 data of Schneider (a relatively low count was obtained on Transect No. 24 in 1976).

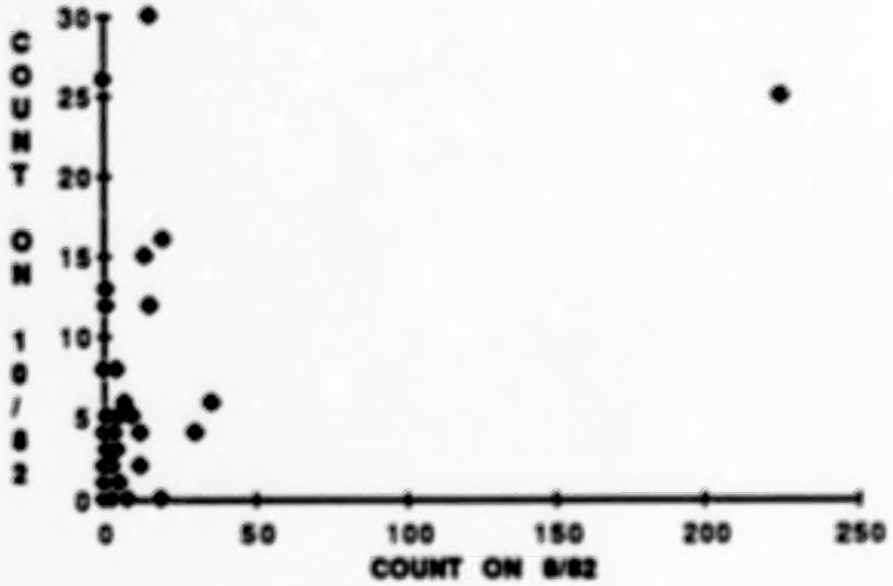


Fig. 3.3 Comparison of sea otter counts in August and October of 1982.

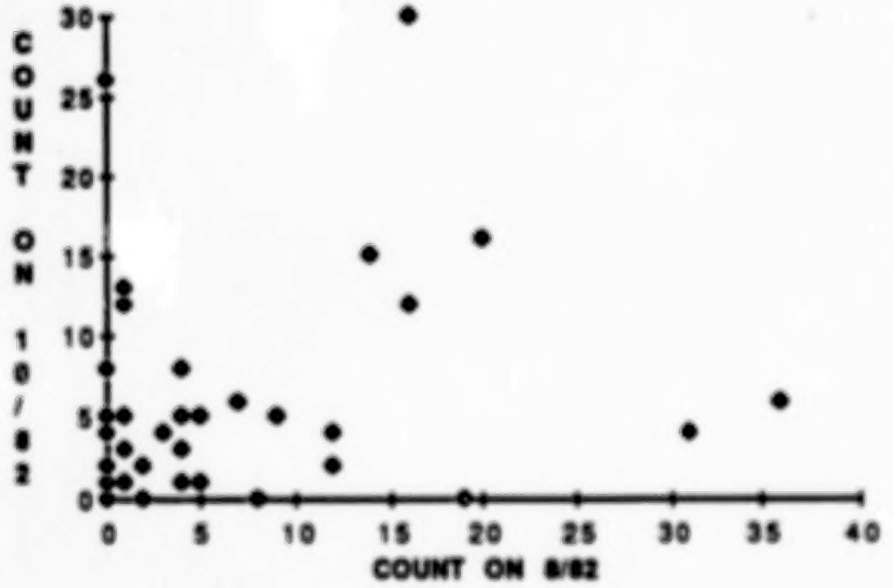


Fig. 3.4 Sea otter counts in August and October of 1982 with Transect No. 24 (226 otters in August of 1982) deleted.

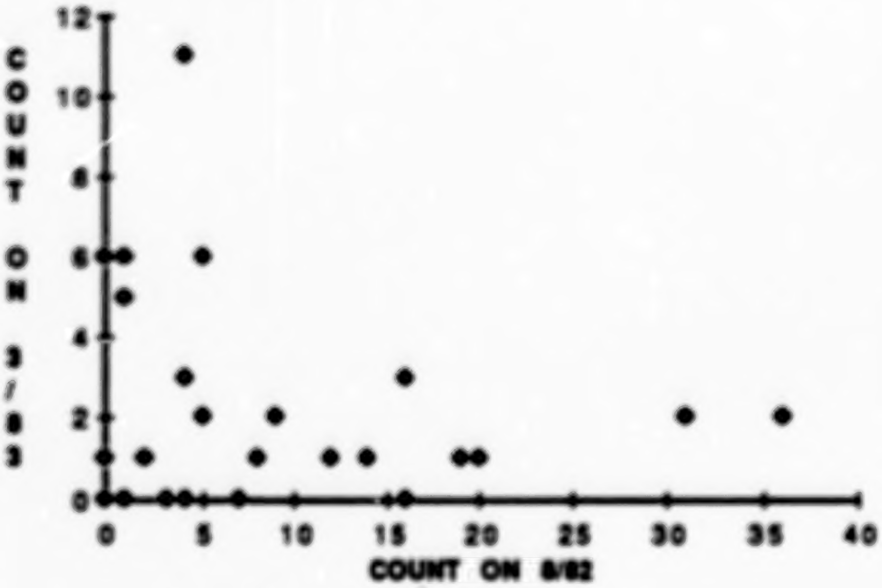


Fig. 3.5 Sea otter counts in August of 1982 and March of 1983, without Transect No. 24 (226 otters in August of 1982).

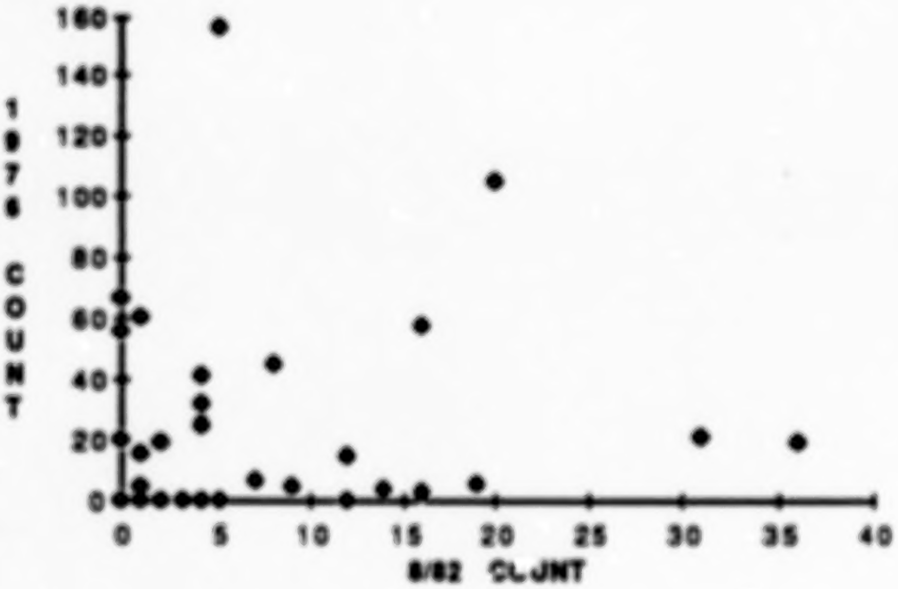


Fig. 3.6 Comparison of sea otter counts in August of 1982 (Transect No. 24 omitted) with counts by Schneider in 1976.

An obvious general conclusion from these comparisons is that the various counts are very poorly correlated, and thus provide little information on consistency of distributions of otters in the study area over time. Since the transects were relatively narrow (0.2 nautical miles in width), it is quite likely that local movements of otters could affect such comparisons. We thus consider the overall pattern of counts in Fig. 3.7 (again without Transect No. 24). This gives a better impression of consistency in the counts, suggesting relatively high concentrations near the central area of the region surveyed.

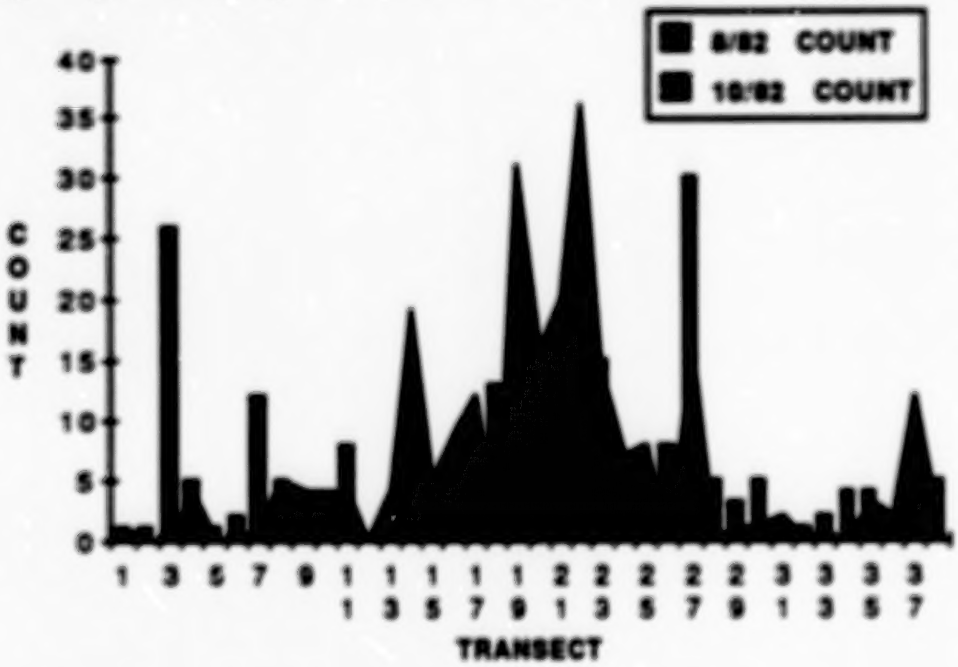


Fig. 3.7 Comparison of counts in August and October of 1982 in serial order, omitting Transect No. 24.

Comparisons between the 1976 survey and the major survey (Aug. 1982) of Cimberg and Costa (1985) are provided by Figs. 3.8 and 3.9, with and without the high count of Transect No. 24. These figures make it clear that the 1976 survey suggests a much greater spatial disperison of otters. Without further information on seasonal movement patterns, it will be virtually impossible to judge whether the population is currently concentrated in a much narrower range than in 1976, or whether these differences may simply reflect chance circumstances, perhaps associated with transient weather conditions.

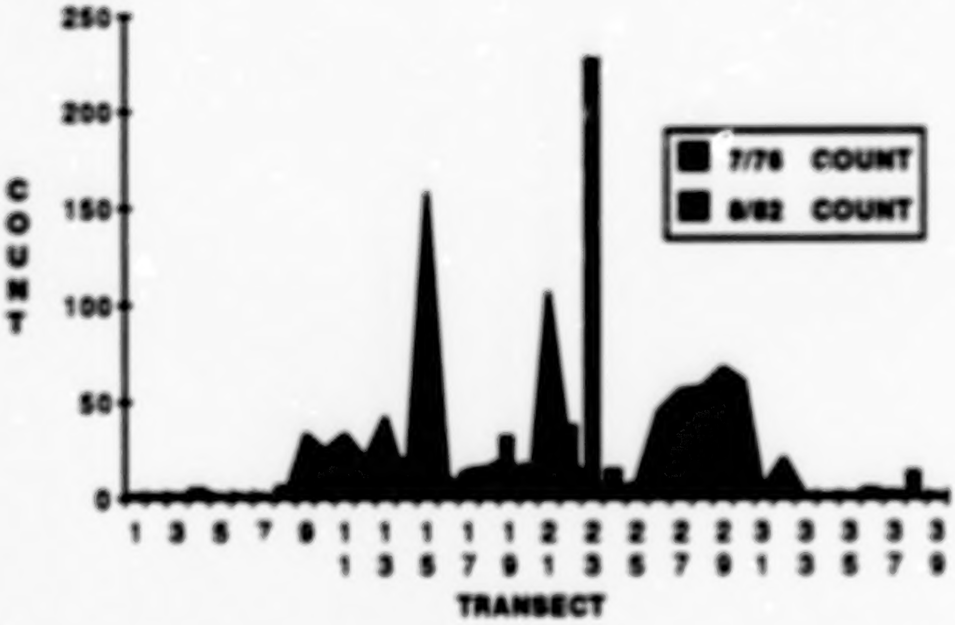


Fig. 3.8 Comparison of 1976 and August 1982 counts, including the high transect (No. 24) of 1982.

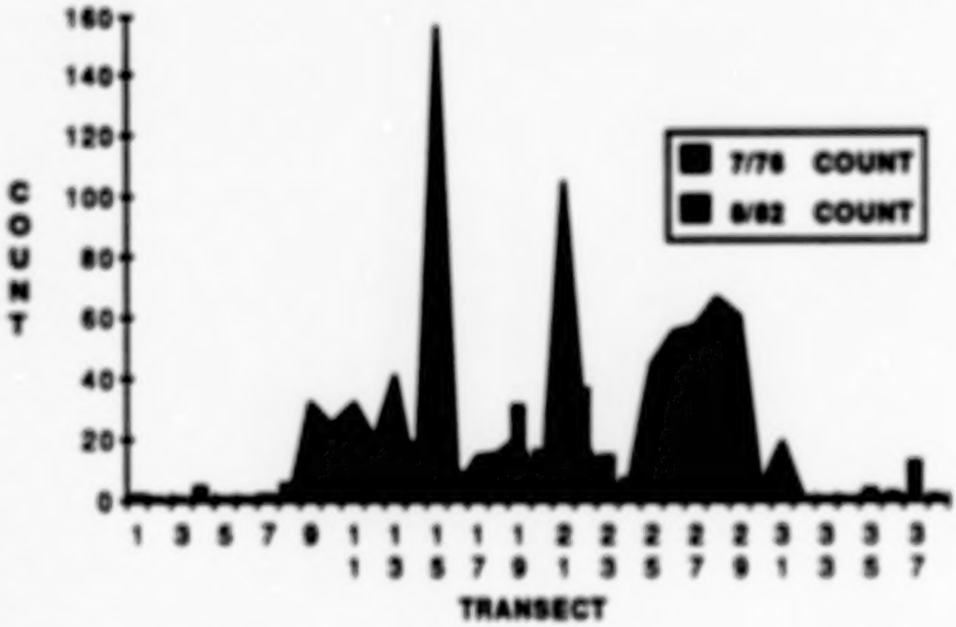


Fig. 3.9 Comparison of 1976 count and August 1982 count without Transect No. 24.

4.0 OIL SPILL EFFECTS

No oil spill modelling was conducted in the present study. Data on oil spill risk assessments for the study area is available in Appendix G of the Final Environmental Impact Statement for North Aleutian Basin Sale 92, USDI, Minerals Management Service, Alaska Outer Continental Shelf Region (September, 1985). Details of a six-year modelling study dealing with hydrodynamic and spill trajectory modelling appear in Liu and Leendertse (1987).

The available information on sea otter populations in the study area indicates that the population may range well out into the Bering Sea to forage. At other times, stormy or inclement weather may result in large concentrations in nearshore areas. Such extensive movements make it important to have a good definition of the likely tracks of any oil spills, since spills drifting across the paths of otter movements to and from foraging areas could be particularly damaging to the population.

4.1 Effects of oil on sea otters

Relatively little information is available on the impacts of oil on sea otters in terms of actual mortality rates. Developing such information experimentally via standard bioassay methods would undoubtedly require the exposure of literally hundreds of sea otters to varying degrees of contamination by oil. A generally-held opinion is that any substantial contact with oil is likely to result in death of the affected individual, unless immediate steps can be taken to remove the majority of the oil. Thus it seems likely that a small range in degree of contamination will correspond to a very wide range of survival. Under such circumstances, it is probable that an "all or none" kind of impact model may be adequate for practical purposes.The incursion of oil into an occupied area may be assumed to remove a fraction of the otter population corresponding to that proportion of the otter range traversed by the oil spill.

More explicit kinds of oil-effects data were suggested by Ford and Bonnell(1986). They cite various references to support the statement that "Laboratory studies suggest that any sea otter oiled over about 25% or more of its surface will probably die from hypothermia if left uncleaned". They have also made estimates of the percent of sea otters that will die from various kinds and degrees of oil contamination. Four classes of oil spill conditions were proposed: (1) relatively thin and patchy slicks of fresh oil in the area of contamination (light oiling), (2) thin and patchy slicks of fairly weathered oil, (3) thick and continuous slicks of fresh oil (heavy oiling), and (4) thick and continuous slicks of weathered oil. A range of mortality was then proposed as:

	Percent Mortality		
Conditions	Low	Most likely	High
Fresh/thick oil	80	90	100
Fresh/light oil	10	40	80
Weathered/thick oil	70	80	100
Weathered/light	10	30	60

They state, however, that "Our estimates of otter mortality at this point can only be described as reasonable guesses which we have discussed with experts having some experience with this subject (D. Costa, D. Siniff, T. Williams, J. Ames, G. Van Blaricom). The wide range in the possible values of these parameters reflects the uncertainty of these estimates ... ". If some sort of direct estimate of mortality is to be used, then these values may be considered. As noted above, we believe that any direct estimates of degree of mortality would require very extensive experimental work, and the best course at present likely is to use the "all or none" approach based on areas of projected oil spill trajectories as they impact sea otter range.

4.2 Incursions of sea ice

A major problem in evaluating oil spill risks to sea otters may be circumstances in which a severe winter results in the incursion of sea ice into the area. As described above, a number of years of such incursions are on record. The main consequence of such conditions appears to be one of a temporary concentration of the sea otter population in a limited area. Under such circumstances, an oil spill might result in very extensive mortality. Consequently, it will be necessary to decide whether such an event can be ruled out on the basis of operational constraints on extraction and transport during periods of ice incursions.

Another feature relevant to oil spill scenarios is that there is relatively little information about the sex and age segregation of otters in the study area. Studies in various other areas have demonstrated distinct seasonal separations of segments of the population. Unless similar information can be developed for the study area, it seems unlikely that small-scale details of either an otter population model or and oil spill scenario will be very useful.

5.0 CONCEPTUAL POPULATION MODELS

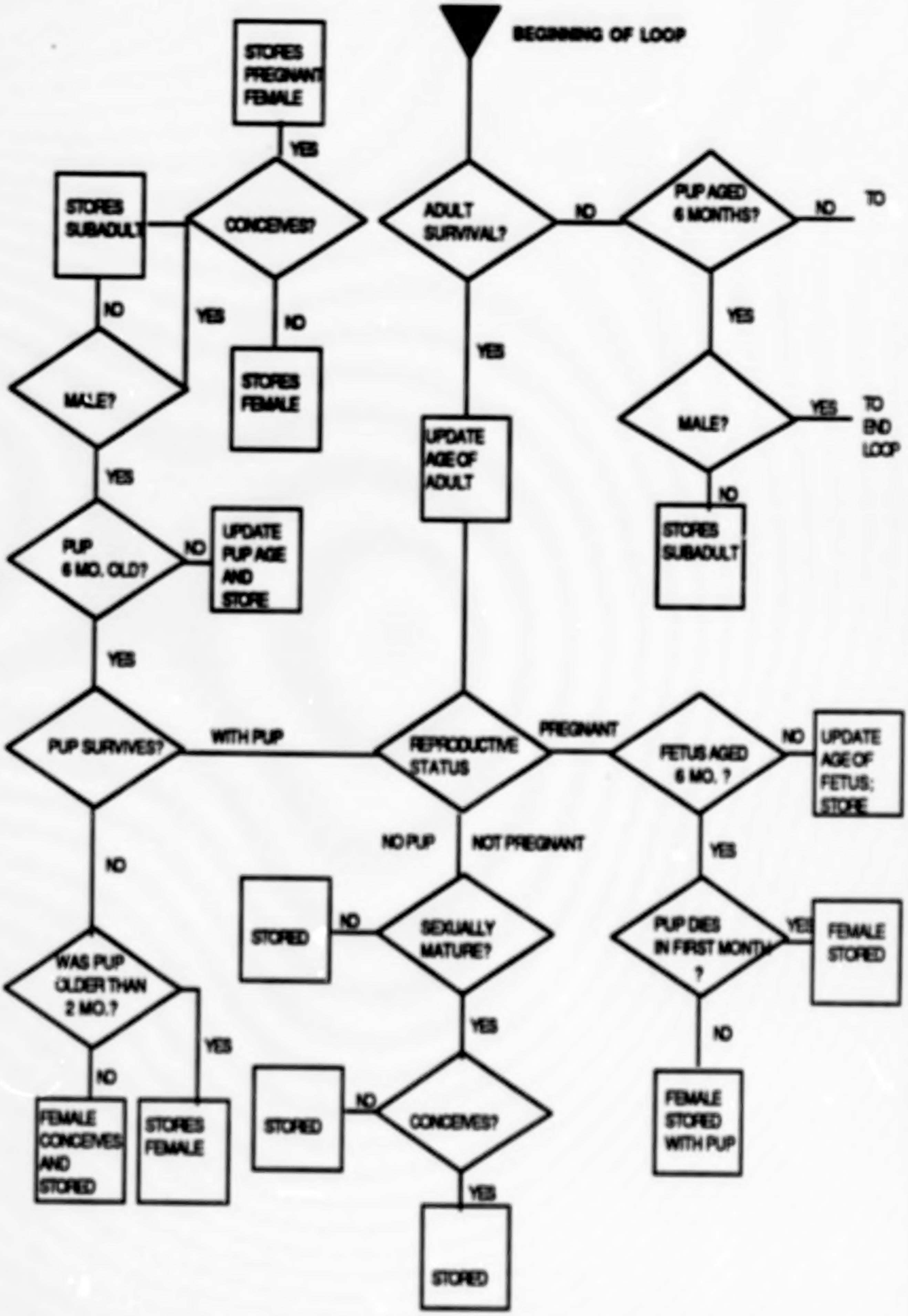
5.1 The California model

The existing population model was developed as a stochastic model, with monthly updating of the fate of individual otters. Each individual is denoted by an 8 digit number (string variable), with the first 3 digits representing the age in months, the fourth, pupping status (no pup, pup, or pregnant), the fifth records age of fetus or pup (1-6 months), and the last 3 digits give location of the otter along the coastline (the California habitat is essentially linear, so only the single coordinate is needed). In the basic model, only females 7 months of age and older are considered individually, since the essential features of population dynamics can be modeled by using only the female segment of the population. Pups are weaned at 6 months in the model, and females then become independent individuals. The model has been maintained as several separate, but interacting, programs to facilitate implementation on microcomputers.

The model is based on nested loops. The innermost processes individuals, the next loop represents months, the third years, and a final loop repeats simulations. The essential operations, contained in the innermost loop, are shown in the flow diagram of Fig. 5.1. Each decision point, represented by a diamond shape in the figure, depends on a random draw, with probabilities structured as described below. Starting at the beginning of the loop (as indicated at the top of the figure), a random draw determines whether or not the individual survives. If not, the diagram to the right of this first diamond determines first whether or not the adult is accompanied by a pup. If so, and if the pup is old enough to survive alone and is a female, it is stored as an independent subadult.

If the original adult survives, the next decision point (diamond at center of page) determines reproductive status (as recorded by the fourth digit of the string variable representing the individual), and the program proceeds to one of the 3 branches depending on reproductive state (pregnant, to the right; pup to the left; neither, below the decision point). Pups are assumed to accompany the female until they are weaned at 6 months, whereupon the pup, if female, is assigned an independent identity.

A number of subroutines serve to perform various auxiliary calculations, such as tabulating and printing out accumulated data at the end of any selected month or year, and supplying storage for data generated in the main program. Another subroutine can be activated at any point in time to generate an "oil spill" at any selected position in the sea otter "range".


BEGINNING OF LOOP
STORES PREGNANT FEMALE
YES
STORES SUBADULT
CONCEIVES?
ADULT SURVIVAL?
NO
PUP AGED 6 MONTHS?
NO
TO
NO
YES
NO
YES
YES
STORES FEMALE
MALE?
UPDATE AGE OF ADULT
MALE?
YES
TO END LOOP
YES
NO
STORES SUBADULT
PUP 6 MO. OLD?
NO
UPDATE PUP AGE AND STORE
YES
PUP SURVIVES?
WITH PUP
REPRODUCTIVE STATUS
PREGNANT
FETUS AGED 6 MO. ?
NO
UPDATE AGE OF FETUS; STORE
NO PUP
NOT PREGNANT
YES
NO
STORED
NO
SEXUALLY MATURE?
PUP DIES IN FIRST MONTH ?
YES
FEMALE STORED
WAS PUP OLDER THAN 2 MO.?
YES
YES
NO
NO
FEMALE CONCEIVES AND STORED
STORES FEMALE
STORED
NO
CONCEIVES?
FEMALE STORED WITH PUP
YES
STORED

Various modifications of the basic model have been developed for use with the California population. Three basic programs were designed, one being the population model as described above, a second a spatial distribution model based on the extensive available historical data on distribution of sea otters along the California coast, and the third a short term movement and oil reponse model.

5.2 Circumstances in the Bering Sea area

As noted above, the California sea otter population inhabits a narrow belt of close-inshore habitat along the California coastline. Most individuals seldom stray more than a kilometer from the shoreline. In contradistinction, otters along the Bering Sea side of the Alaskan Peninsula and Unimak Island appear at times to adopt virtually a pelagic existence, being found as much as 40-50 km out to sea. Distributional data in California are available from some 30 to 40 individual censuses and counts over a long span of years, most of which suggest a relatively stable pattern of distribution, with some seasonal shifts. The available data on the Bering Sea population amounts to relatively few transect counts, with the suggestion of an appreciable difference between 1976 and 1982. A very substantial array of demographic and biological data has been accumulated on the California population over 2 decades of study, and extensive telemetry data have been obtained in recent years.

With these substantial differences in the two areas, it does not seem sensible to attempt to adapt the California model for the Alaskan situation. It would be quite feasible to construct a similar model, but the dramatic difference in spatial configuration of the two populations would require extensive restructuring of the entire model, going from essentially a linear structure to one operating in two dimensions. A much better use of time and other resources is thus to construct a simpler model designed to operate with the much more limited data set available in Alaska.

The final version of the redesigned model depends on results of the extensive analysis of available data for parameter estimation, discussed in succeeding sections of this report, and inputs on hypothetical oil spills. The results of the analyses for parameter estimates and the oil spill scenarios should dictate structure of the model if realistic outcomes are to be obtained. The most useful model will be one with a few large, interconnected populations. Such a choice is dictated by two considerations. The first is the limited detail on spatial distribution of the population, and the second is that we suspect that the most effective depiction of many possible oil spills is simply that a given area of water surface will be impinged on by oil. Another consideration will be the needed decision on how to accomodate the possibliity of an ice incursion in conjunction with an oil spill. If such a circumstance is to be incorporated, it is likely that the otter population will have to be considered as a single aggregate, at least during the period of an incursion.

5.3 The conceptual approach

The conceptual approach for this study is essentially a three-step process (Fig. 5.2). The first stage is devoted to testing assumptions and hypotheses based on the available data (as described in previous sections of the report). The next stage utilized that data shown to be internally consistent in stage 1 as a basis for generating parameter estimates, and the final stage is a simplified Leslie matrix model used to generate outcomes for various oil spill scenarios.

CONCEPTUAL APPROACH

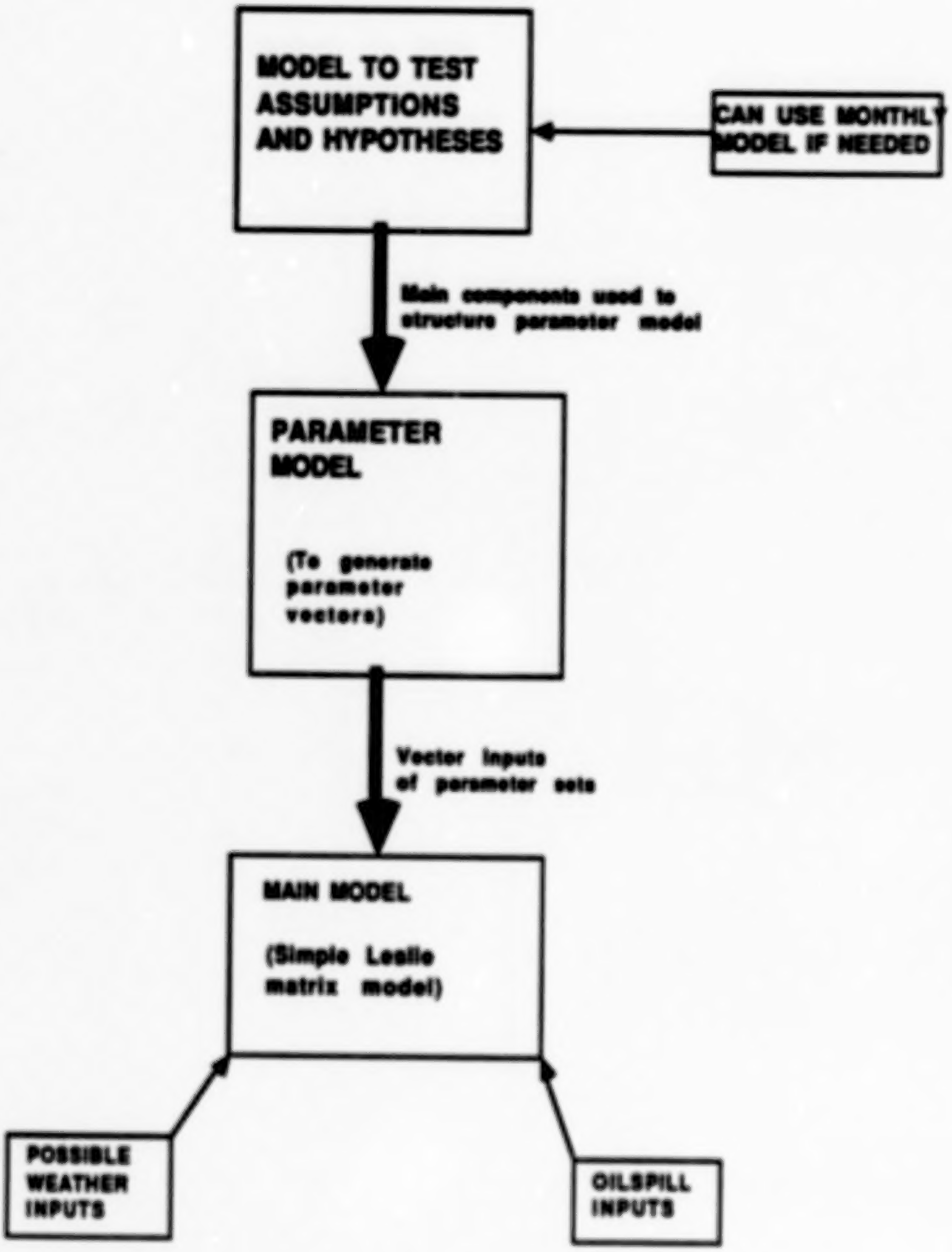

MODEL TO TEST ASSUMPTIONS AND HYPOTHESES
CAN USE MONTHLY MODEL IF NEEDED
Main components used to structure parameter model
PARAMETER MODEL
(To generate parameter vectors)
Vector inputs of parameter sets
MAIN MODEL
(Simple Leslie matrix model)
POSSIBLE WEATHER INPUTS
OILSPILL INPUTS

FIG. 5.2 CONCEPTUAL APPROACH FOR SEA OTTER MODELLING STUDY

6.0 ASSUMPTIONS AND INITIAL CONDITIONS

As already discussed here, we do not believe that it is possible to effectively develop a suitable range of assumptions from site data alone. At present most of the essential parameter estimates are not available for the study site. We have almost no information on survival rates or reproductive rates in this population. A population survey in 1976 (Schneider 1976) estimated about 17,200 otters in the Bering Sea population, while Cimberg and Costa estimated about 10,300 present in 1982, and more recent estimates indicate a population of 13,090 (Bruggeman 1987). Since this is the only direct data on demographic conditions in the area, a realistic range of assumptions might well be argued to be one including a continuing decline in population size. An oil spill could thus simply result in a lower population, with no recovery. We doubt that such a scenario is reasonable, but mention it to emphasize the need for further efforts to estimate population parameters at the site.

6.1 General procedure for developing assumptions

Basically, parameter estimates for modeling have been obtained from data on other sea otter populations. The most useful procedure would seem to be one of deriving such estimates and then searching for ways to test the hypothesis that rates or circumstances in the study area do not differ significantly from those estimated elsewhere. The most reliable tests will very likely be those based on continued acquisition of data on otters in the area by telemetry. Thus far, the only telemetry instrumentation has been in Bechevin Bay, and has further documented the indications developed by Schneider (1976) of a breeding and "nursery" area in the Bay and the area just offshore, with likely feeding and other excursions to the west along Unimak Island and to the east towards Izembek Lagoon. Distribution of population counts in the two major surveys is shown in Fig. 5.1. Two main concentration areas were defined by Schneider to lie in areas corresponding to locations where the bulk of the 1976 counts were recorded, or into roughly eastern and western populations. We thus suspect that a minimal subdivision for modeling purposes may be into two such populations.

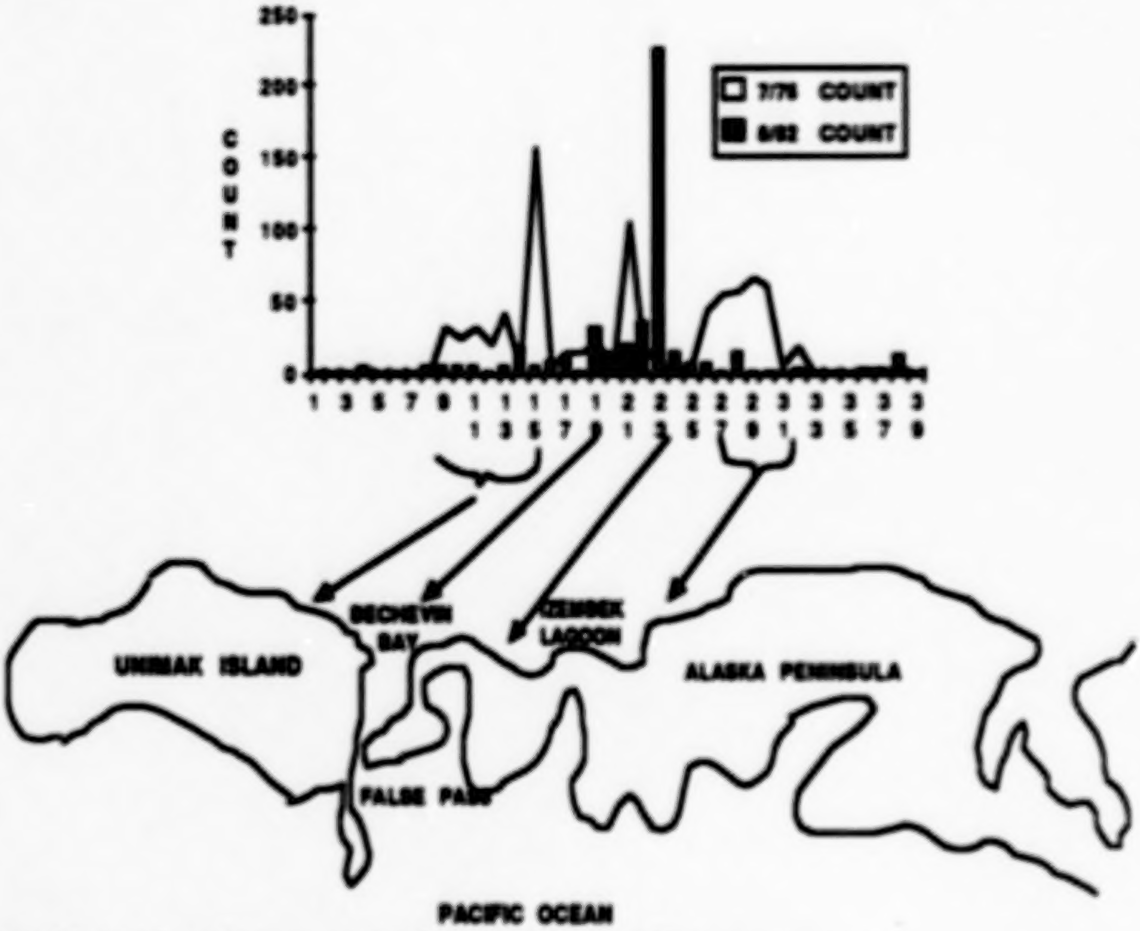


Fig. 6.1. Locations of concentrations of sea otters as indicated by transect counts.

6.2 Parameter estimates needed

A brief review of parameter estimates needed follows, to give some further indications of data requirements and possible tests of the hypothesis that such estimates can be based on data from other sea otter populations, and yet remain appropriate for the study area. The initial population size is less important from the standpoint of predicting oil spill effects than is the spatial distribution of the population. If the breeding population is concentrated in the area of a spill, then a very long period of recovery may be required to reach the same relative level as prevailed before the spill. For reasons discussed earlier, it is likely that the various surveys have underestimated actual population size, so the model most likely should be considered in terms of relative population sizes in any case.

Reproductive parameters will mainly include pupping rates and age of first reproduction. The most important issue here has to do with frequency of reproduction. Virtually all published reports on Alaskan otters assume mature females will pup every second year, whereas there is a good deal of evidence that California otters pup annually. It thus appears that the reproductive rate in Alaska might be roughly half of that observed in California. Something of an anomaly obviously exists here, since it is also generally assumed that many of the Alaskan populations have increased at rates substantially exceeding the 5 percent per year rate estimated for California. Part of the difficulty may depend on the fact that the most extensive data for reproductive rate estimation comes from samples of otters shot in the Aleutians, often from populations that likely were food-limited. It is conceivable that reproduction might be reduced sharply in such populations.

Hence, we have investigated recent indications that the data may actually support annual reproduction.

Another factor that needs to be considered is that the tendency of otters to reproduce throughout the year makes derivation of reproductive rates very difficult, especially if sample sizes in some parts of the year are limited. We thus will need to do a substantial amount of further analysis of the data available to provide suitable comparisons between the Alaskan and California data. Also, as previously noted, it will be essential to try to determine whether the study area populations may be characterized by data collected further out in the Aleutian chain. The available biological data suggest that the study area population is in very good physical condition, so that rates observed at Amchitka Island, for example, may not be typical for the study area.

Survival rates are the most difficult parameters to obtain for virtually any wild population. Rates for sea otters have mostly been speculative, and only recently have bona fide estimates begun to be available through telemetry. Early survival rates are particularly difficult to obtain, but have been developed for the California population on the basis of relative ratios of small and large pups, and from limited telemetry data. Enough telemetry data to obtain rough estimates of survivorship are now beginning to be available for Prince William Sound, and we believe that it is important to try to check these by increasing the sample in the Bering Sea study area.

A final major problem in parameter estimation concerns density-dependence and carrying capacity. It is generally assumed that otter populations are food-limited, but the exact nature of the limitation thus imposed on population growth is largely a matter of speculation.

7.0 SURVIVAL ESTIMATES

The essential parameters for modelling sea otter population dynamics are those having to do with survivorship and reproduction. We first assess the observational data available that can be used for both indirect and direct estimates and then consider additional information obtained by radiotelemetry.

7.1 Survival estimates from age structure data

The survivorship model used here is one assessed by Eberhardt (1985:eq.(6)):

$$l_x = e^{-F - Gx - D(\exp(Ex) - 1)} \qquad (7.1)$$

where l_x denotes survival to age x, F is a parameter concerned with early survival, G denotes adult survival, and D and E control the onset and duration of senescence. Two approaches to fitting data to reproductive and survival curves need to be considered. The usual one is to code ages 0,1,2,3,... with age 0 being newborns. For present purposes ages (x) are coded 0,1,2,3,...., with age 0 denoting age at weaning (about 6 months old), age 1 then being 18 months, age 2, 30 months, and so on. This arrangement is needed because most of the field observations classify individuals as either "independent" (free-swimming) otters or as dependent pups. Hence recruitment to the population (of independent otters) is defined as taking place at 6 months of age, and the most intensive early mortality occurs before recruitment. Reproductive rates thus will need to be based on birth rates multiplied by survival to 6 months of age.

7.2 Aleutian age structure data

The age structure data used here were reported by Schneider (1978:Fig. 2) and were from collections made in an experimental harvest program in the western Aleutian Islands in September and October, when relatively few pups were present. From the observed age structure, it is evident that subadults (ages 1-3) were not present in the female areas in proportion to their actual abundance (Fig. 7.1). Consequently further analyses are restricted to individuals age 4 and older. Ages were determined by sectioning and counting tooth cementum layers (Schneider 1973).

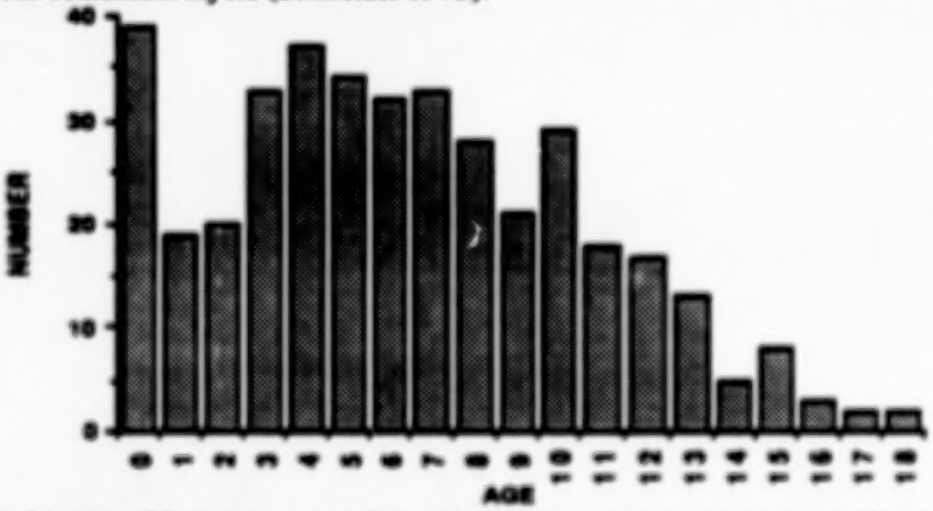


Fig. 7.1. Ages of female sea otters collected in the western Aleutian Islands in experimental harvests in September and October in "female" areas, prior to 1972.

Survival of female otters between ages of 4 and 10 was estimated by the "segment" method described by Chapman and Robson (1960), giving an estimate of annual survival of 0.939, with a standard error of 0.032, and a relatively good fit to the data (chi-square of 2.09, 6 d.f.) as is evident in Fig. 7.2. A somewhat lower rate was estimated for ages 4-12 (S= 0.915, S.E.= 0.028, chi-sq.= 3.47).

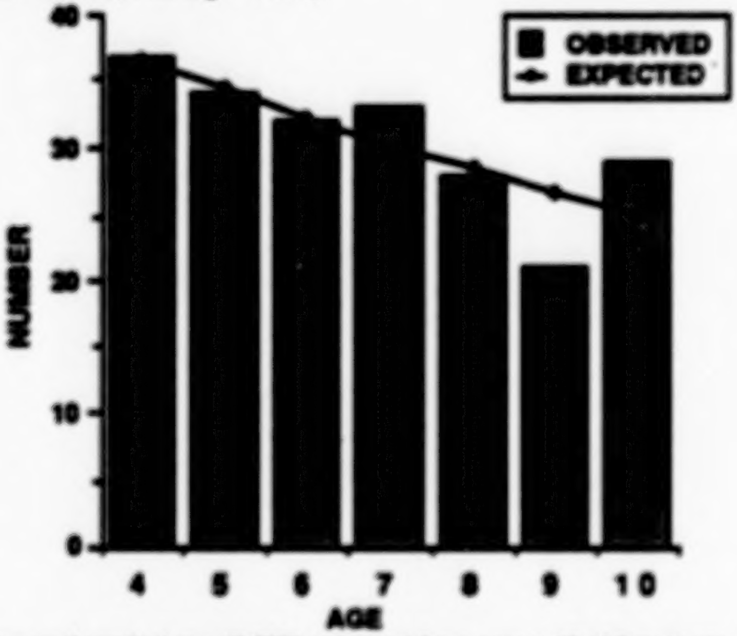


Fig. 7.2. Constant annual survival rate (0.939) estimated from ages 4-10 of female sea otters in western Aleutian Islands.

Survival rates drop off appreciably if older animals are included in the sample, so eq. (7.1) was used to investigate the likely effect of senescence. The parameter (F) relating to early survival need not be considered, inasmuch as we can denote the number (n_x) in a given age class as:

$$n_x = n\frac{e^{-F-Gx-D(\exp(Ex)-1)}}{\Sigma\, e^{-F-Gx-D(\exp(Ex)-1)}} = n\frac{e^{-Gx-D(\exp(Ex)-1)}}{\Sigma\, e^{-Gx-D(\exp(Ex)-1)}} \qquad (7.2)$$

where the summation is over ages 4 to 18, and there are assumed to be n otters surviving to age 4 (and thus constituting the sample of interest here). The 3 parameters (G,D, and E) were then estimated by varying these 3 parameters until a minimum chi-square was obtained between observed age frequencies and those estimated from eq.(7.2). For convenience, the senescence parameters (D and E) were expressed in a somewhat more intuitively understandable forms; $D = \exp(-T/S_T)$ and $E = 1/S_T$, where T is the "modal age of senescent death" and S_T is its standard deviation (cf. Siler(1979)), while G was expressed as a survival rate, $S = e^{-G}$. Parameter estimates giving a minimum chi-square value (6.52) were S= 0.982, T = 13, and S_T = 4.2. These 3 parameters give a very good fit to the observed data (Fig. 7.3). The BASIC program (ALEUT1) used for the calculations is listed in the Appendix (Sec. 11.4).

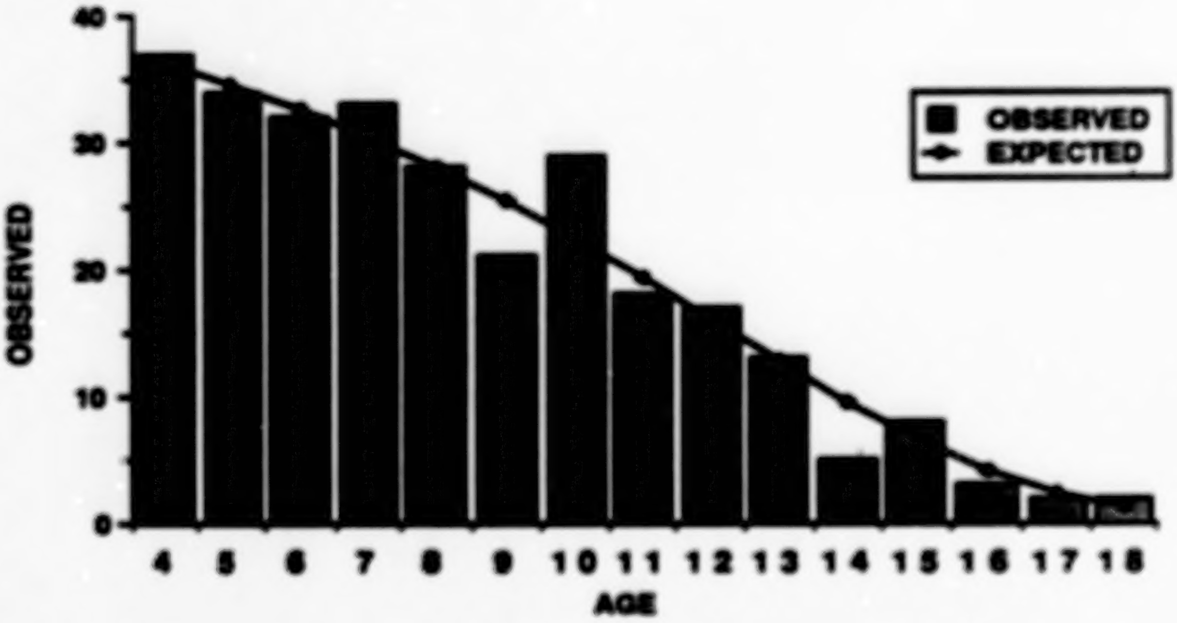


Fig. 7.3. Fit of a survivorship curve (eq.(7.1)) to ages of female otters collected in the western Aleutian Islands.

A difficulty here is that survival rates calculated from eq.(7.1) using these parameters will differ substantially from the constant rate estimated by the Chapman-Robson method. This can be illustrated (Fig. 7.4) by comparing the expected values of Fig. 7.2 with those of Fig. 7.3. Clearly, the 3 parameter fitted curve does not agree with the constant survival rate obtained by the Chapman-Robson method.

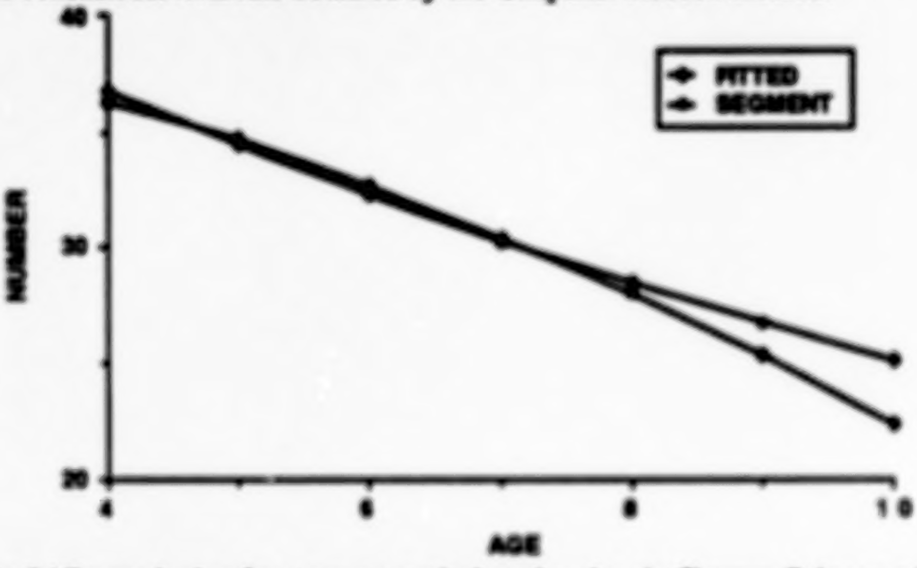


Fig. 7.4 Expected values for a constant survival rate based on the Chapman-Robson method (Fig. 7.2) compared with those calculated from a curve incorporating senescence (Fig. 7.3).

The basis for the problem can be exhibited by examining "senescence functions", $e^{-D(\exp(Ex)-1)}$, for different values of the standard deviation (S_T) of the modal age of senescent death (T). Such a plot (Fig. 7.5) shows that the larger values of S_T result in the effect of senescence being apparent at relatively early ages.

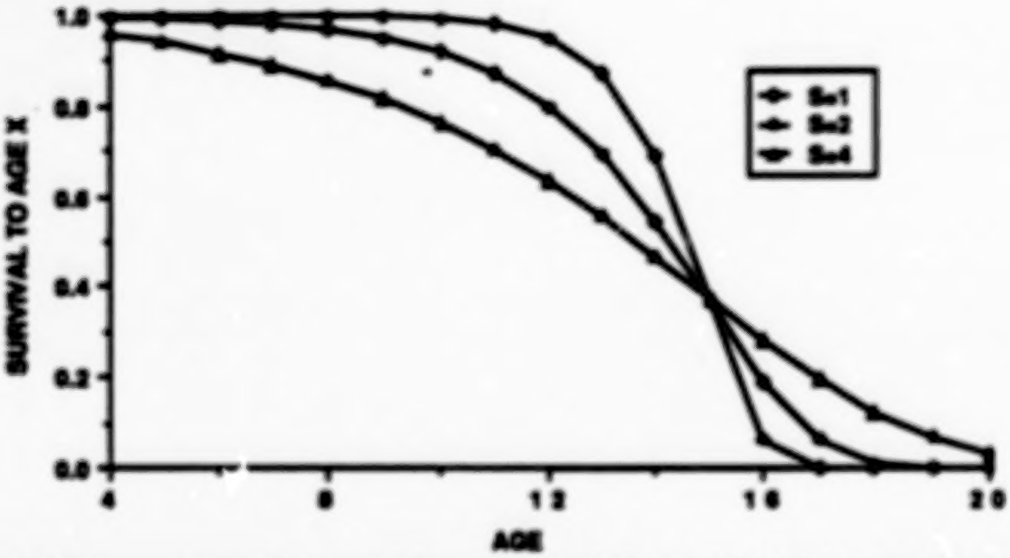


Fig. 7.5. Senescence curves for several values of the standard deviation (S_T) of the modal age of senescent death (T). The modal age was set at T=15 for these curves.

An alternative approach to the data is to use a curve that maintains a constant survival rate until relatively late in life. A small independent sample of ages at death for captive sea otters (Dr. Murray Johnson, personal communication) suggests a modal age of death as T=15. If we also use a corresponding standard deviation of $S_T = 1$, then Fig. 7.5 indicates that there will be little effect from senescence until about age 12. Using the annual survival rate from the Chapman-Robson segment method fitted to ages 4-12 (S=0.915) and T=15, S_T=1 yields a curve with a nearly constant survival rate for ages 4-10 and of the same general shape as the age data (Fig. 7.6), but that underestimates the numbers in the oldest age classes. A listing of the program (ALEUT2) used to produce the fit of Fig. 7.6 appears in the appendix (Section 11.6), along with the output data.

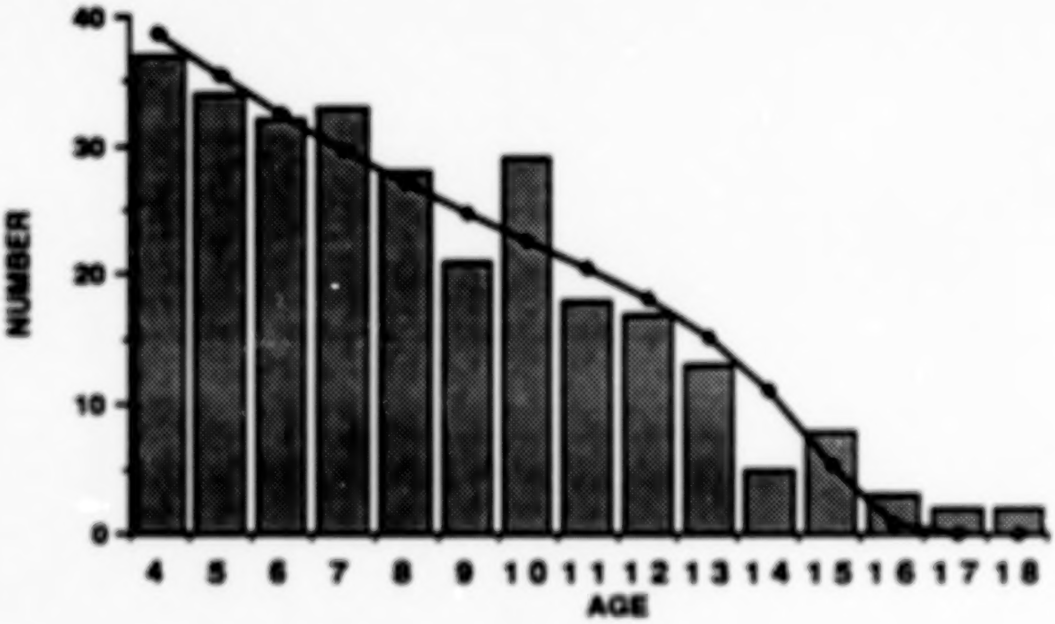


Fig. 7.6. Survivorship curve for female Aleutian sea otters based on annual survival of S=0.915, modal age of senescence of T=15, and standard deviation of S_T=1.

It seems evident that the curve of Fig. 7.3 provides a somewhat better fit but it is also quite likely that accuracy in aging is much less satisfactory for the older age classes. There is also the possibility that some of the oldest females may be reproductively inactive, and thus possibly not located in the "female areas".

7.5 California age structure data

The age data available from California are ages at death, rather than samples from the living population. The California Department of Fish and Game has collected carcasses of sea otters found dead for many years. Skulls from many of these otters were given to local museums, and a tooth was subsequently extracted for age determination. Age structures are available for both male and female otters (Fig. 7.7). An unexplained anomaly in the female data is that, with the exception of animals aged 5, numbers of individuals in the even ages (2,4,6,...) are higher than in the odd-numbered age classes.

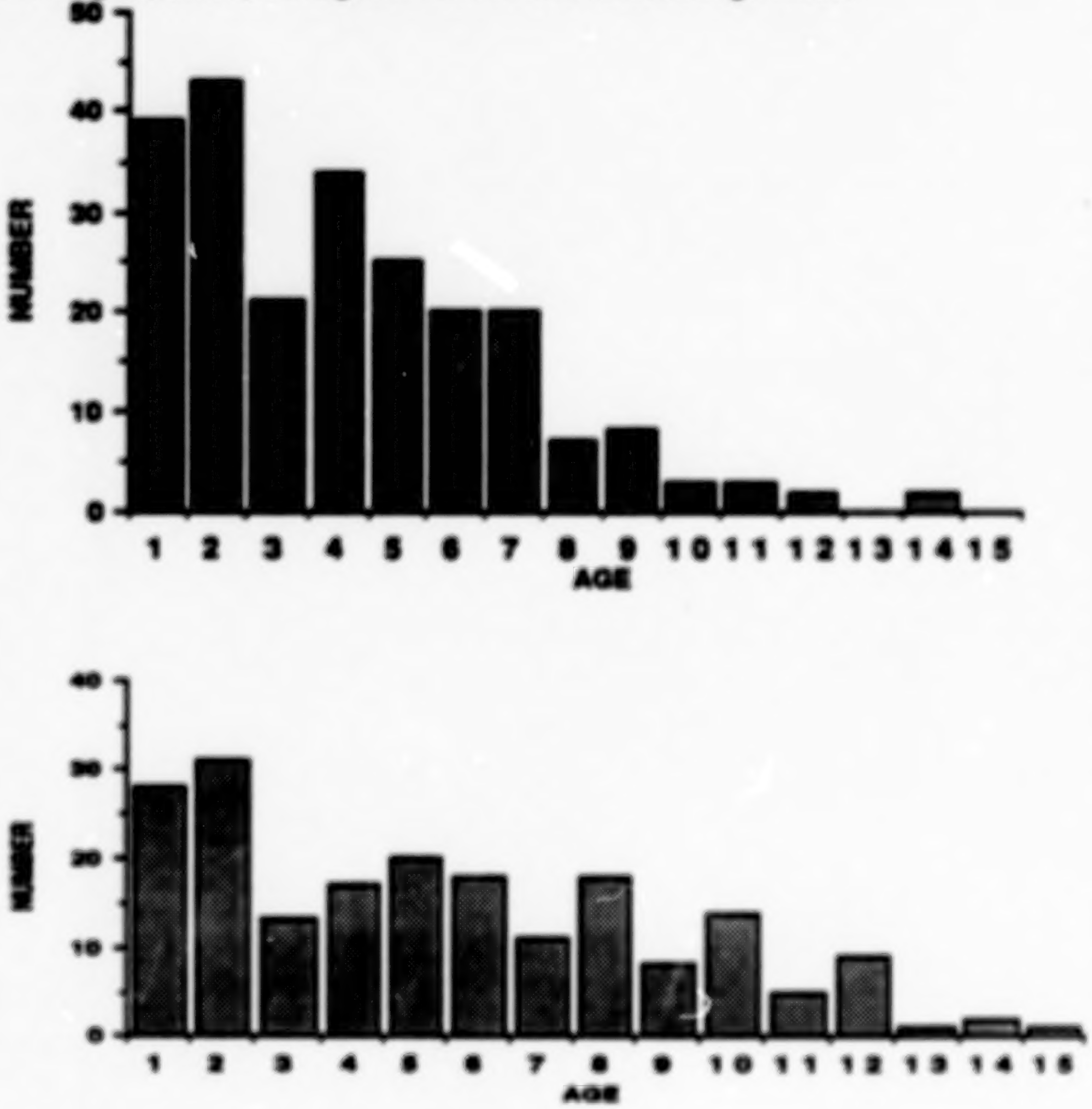


Fig. 7.7 Ages of sea otters found dead along the California coast. Males in upper panel, females in lower panel.

If we let d_x represent the proportion of sea otters dying in year x to x +1 of life, then $d_x = l_x - l_{x+1}$. If the population is stationary and of size N, then the number dying after age 4 is just $n = N\,l_4$ and we can calculate the number dying at age x ($x > 3$) as:

$$n_x = [n/l_4][l_x - l_{x+1}] \tag{7.3}$$

If l_x is as given in eq.(7.1), then the parameter F cancels in numerator and denominator, and we can use a computer search to estimate the remaining 3 parameters, as done in conjunction with eq. (7.2).

If survivorship remains constant beyond some age (c), then $l_x = l_c s^{x-c}$ and the number dying in the interval is:

$$n_x = N(l_x - l_{x+1}) = N(l_c s^{x-c} - l_c s^{x+1-c})$$

$$= N l_c (1-s) s^{-c} s^x = (\text{constant})\ s^x \tag{7.4}$$

so that the Chapman-Robson "segment" method (Chapman and Robson 1960) can again be used to estimate annual survival over that period where s is essentially constant. Adult female survival is estimated as S=0.925 (0.045) for ages 4-10 and the corresponding male survival is 0.723 (0.038). The results (Fig. 7.8) yield a relatively poor fit for females due to the previously-mentioned tendencies for even-numbered ages to be most numerous, excepting age 5. The same sort of difficulty (Fig. 7.9) is evident when the senescence function is incorporated and fitted using eq. (7.3), using the BASIC program of Sec. 11.4. The results given by the Chapman-Robson method are, however, supported by telemetry data. Siniff and Ralls (1988:Ch.2) report an adult female survival rate of 0.91 for adult females and 0.61 for adult males, based on telemetry data. Small samples (16 adult females and 9 adult males were available) and confidence limits were correspondingly wide. These data are considered further in Section 10 of this report.

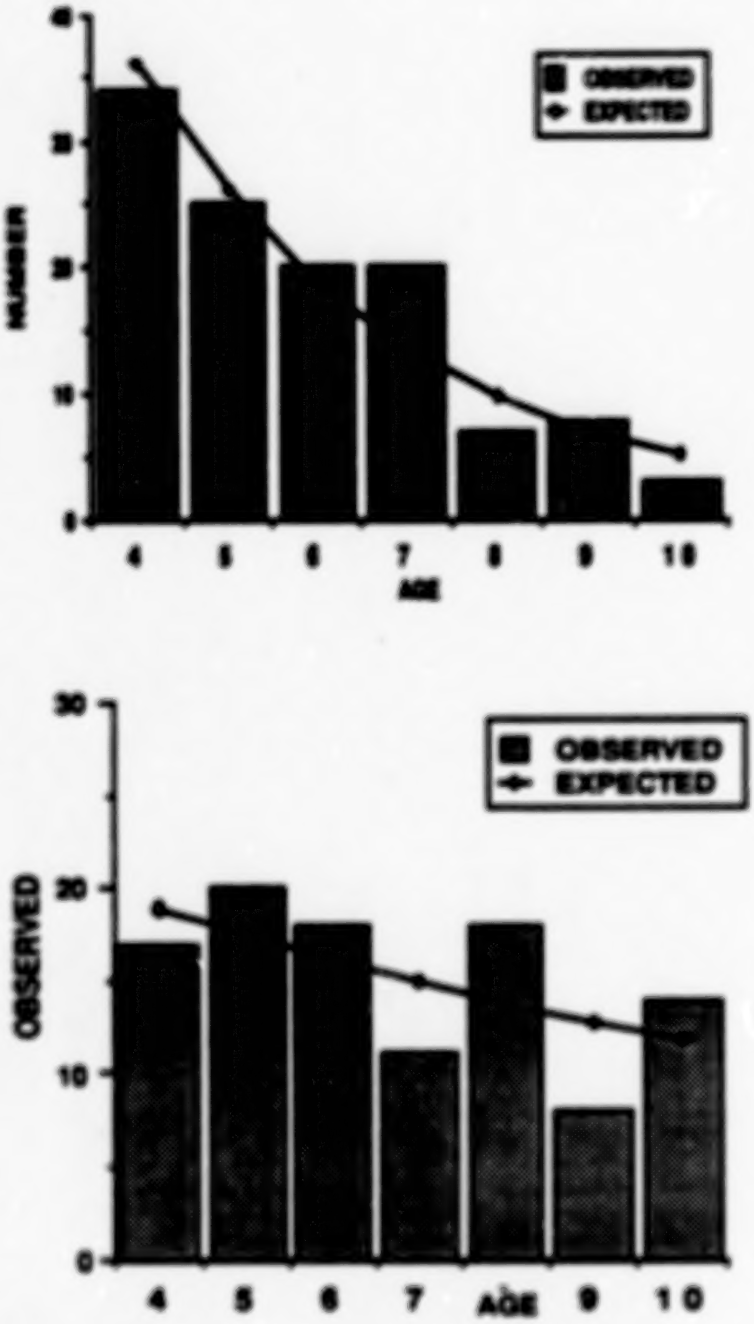


Fig. 7.8. Constant survival by Chapman-Robson segment method fitted to data on ages at death for California sea otters. Males in upper panel, females in lower panel.

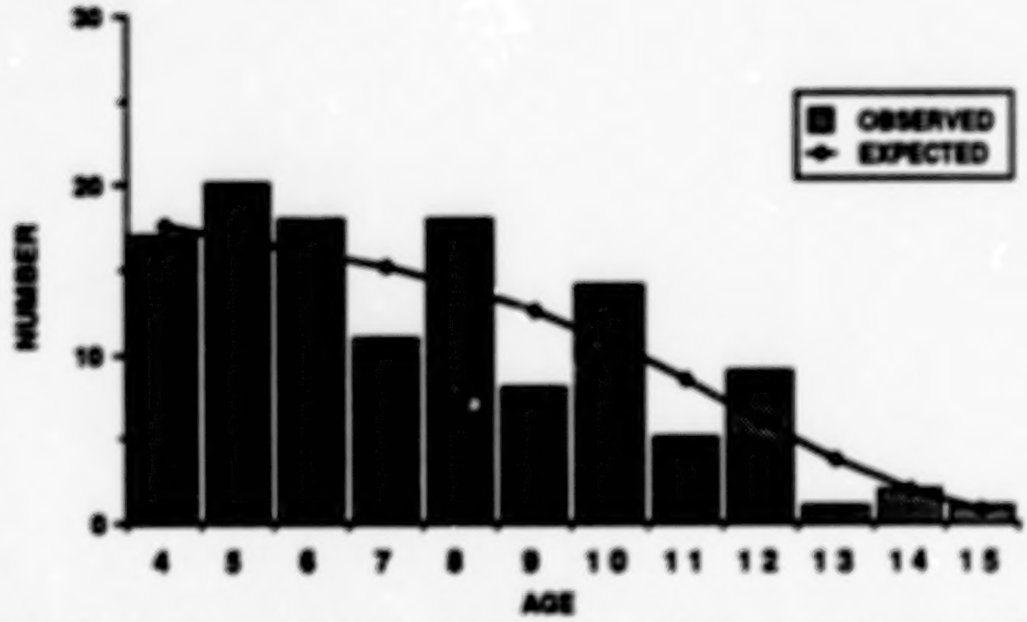


Fig. 7.9. Survivorship curve fitted to ages at death of female California sea otters (S=0.908, T=10.1, S_T=3.6).

The early modal age of senescence (T=10.1), combined with a high standard deviation (S_T = 3.6) results in reduction of adult survival rates to improbably low levels. One possible explanation is simply that the older animals were not adequately represented in museum collections. If we use the parameters calculated for the Aleutian age structure data (T=13, S_T=4.2, and S=0.982), then the resulting expected curve for ages at death (Fig. 7.10) is not at all in accord with the observed data. Changing the senescence parameters to those (T=15, S_T=1) used to produce Fig. 7.6 and maintaining adult survival at the rate (0.925) obtained from the California age data gives the outcome shown in Fig. 7.11. Here it appears that the expected curve adheres to the trend of the observed age structure for ages 4-10, but that most of the older animals are simply missing from the sample examined.

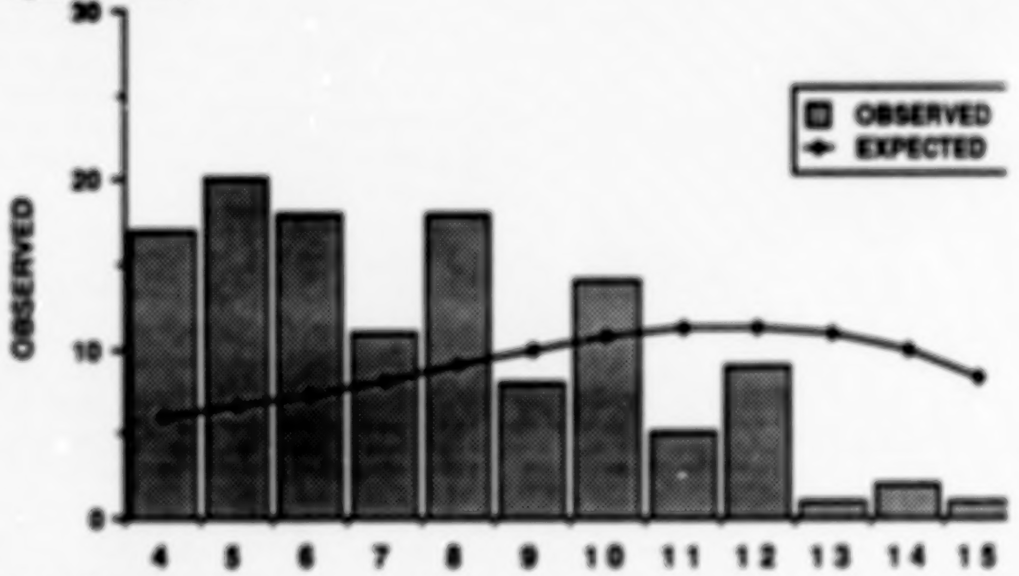


Fig. 7.10. Expected distribution at age of death using parameters estimated from Aleutian Island data (T=13, S_T=4.2, S=0.982) compared with observed ages at death for California
female sea otters.

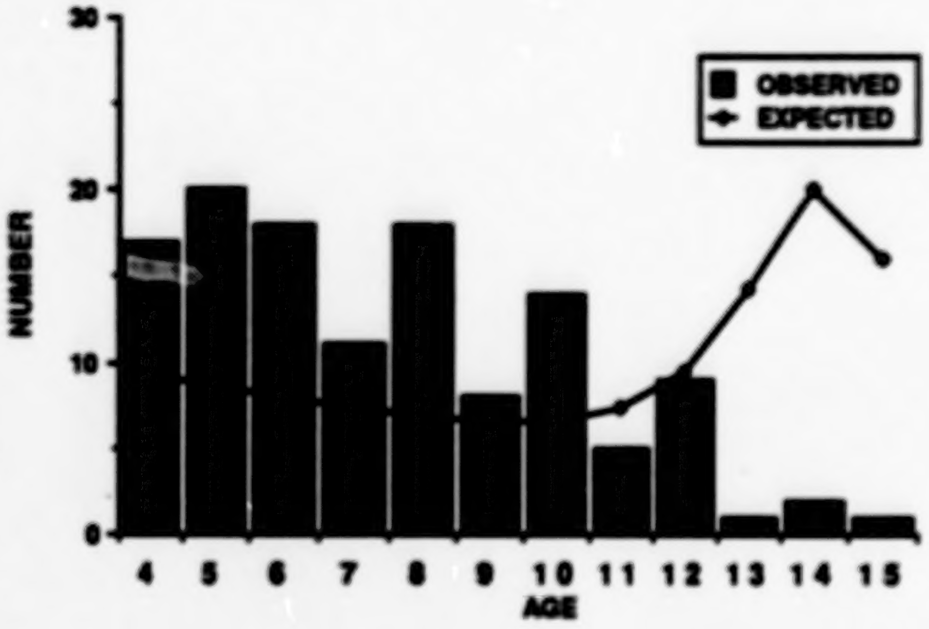


Fig. 7.11. Expected distribution at age of death using senescence parameters (T=15, S_T=1) used for Fig. 7.6 and survival rate (S=0.925) obtained from Chapman-Robson method compared with observed ages at death for female California sea otters.

The remaining alternative for analysis of the California age data is to assume that senescence is not involved at all, i.e., that adult survival is constant beyond age 4. Using the Chapman-Robson method, this gives adult female survival as S=0.778 (0.018). Not only is agreement of observed and expected frequencies (Fig. 7.12) unsatisfactory (chi-square =30.0), the estimated survival rate appears unreasonably low.

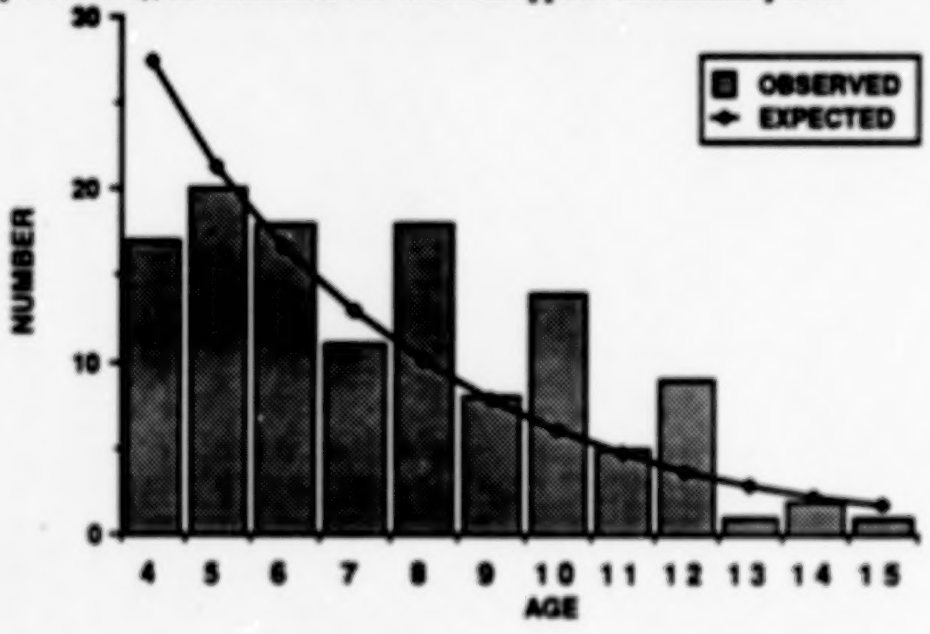


Fig. 7.12 Fit of Chapman-Robson survival estimate ("complete" method) to ages at death of female California sea otters (S=0.778, S.E.=0.018).

7.4 Estimate of early survival rates

One additional estimate that may be attempted from the California age data is the parameter (F) representing early survivorship in eq. (7.1). Since there is reason to question representation of older animals in the sample, as discussed above, the sample is truncated at age 10. We can thus neglect senescence, so that $l_x = e^{-F-Gx} = S_0 S^x$ for ages 1-10. We thus assume the proportion dying by age x is $1-e^{-F-Gx}$ and the proportion of those aged 1 or 2 in the sample aged 1-10 is:

$$p = \frac{1-e^{-F-2G}}{1-e^{-F-10G}} = \frac{1-S_0 S^2}{1-S_0\, S^{10}} = \frac{59}{178} = 0.3315.$$

Using S=0.925 as estimated earlier by the Chapman-Robson method for ages 4-10 gives:

$$\frac{1-0.8556\ S_0}{1-0.4586\ S_0} = 0.3315$$

which can be solved by trial and error to give $S_0 = 0.95$ (F=0.0513). We can then calculate survivorship to age 2 as $S_0S^2 = 0.95(.925)^2 = 0.813$. Siniff and Ralls (1988:Ch. 2) report a survival rate for "juvenile" females based on telemetry data of either 0.75 or 0.80, depending on assumptions used in evaluating the telemetry data.

A major uncertainty in the calculation above is the relatively low frequency of individuals one year of age in the observed data. In both male and female samples there are fewer 1-year olds than 2-year olds. There is thus the possibility that these younger animals may not be properly represented in the age structure sample. Two possible explanations may be advanced. One is that the smallest dead otters do not appear in the sample in proportion to their abundance, as evidenced by the low frequency of pups recorded in the overall sample. A second possibility is that incomplete dentition in some of the 1-year olds might have resulted in selection against them when teeth were extracted from museum specimens for the sample to be aged.

7.5 Stationarity and age structure data

An essential assumption for use of the age structure data for estimating survival rates is that the population be "stationary", i.e., remain at a constant size while the observed age structure developed. If this is not the case, then a correction for the rate of increase is required.

Little information is available on the status of the populations from which the Aleutian age structure data was extracted. Perhaps the best information is that for Amchitka Island (Fig. 3.2), discussed in Section 3.2. Schneider (1978:2) reported that "In most cases these populations had already rapidly increased, reached their peak and then declined to more moderate levels. Most appeared to be regulated by food availability. Therefore, the following discussion ... concerns populations that are at or near 'carrying capacity' in high quality habitat and may not apply to other presently expanding populations".

In the case of California, there is fairly extensive data to suggest that the population has been essentially stationary during most of the period of collection of age structure data. Since the number of dead otters increased quite rapidly in the later stages of the collections, it seems likely that the age structure data should largely represent a stable age distribution. The available information on population trend comes from different surveys in two periods. The first (Fig. 7.13) covers the period 1976 to 1982, and is from several segments of the main otter range. The second source covers the period 1982 to 1985 (Fig. 7.14) and is based on so-called "complete" counts of the otter range.

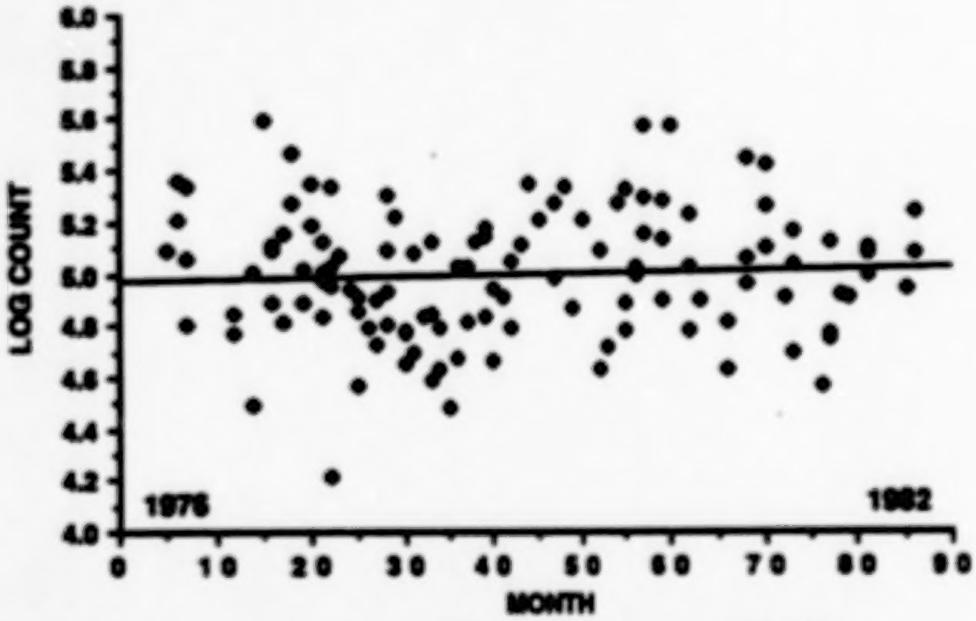


Fig. 7.13. Index counts of selected areas of California sea otter range, 1976-1982.

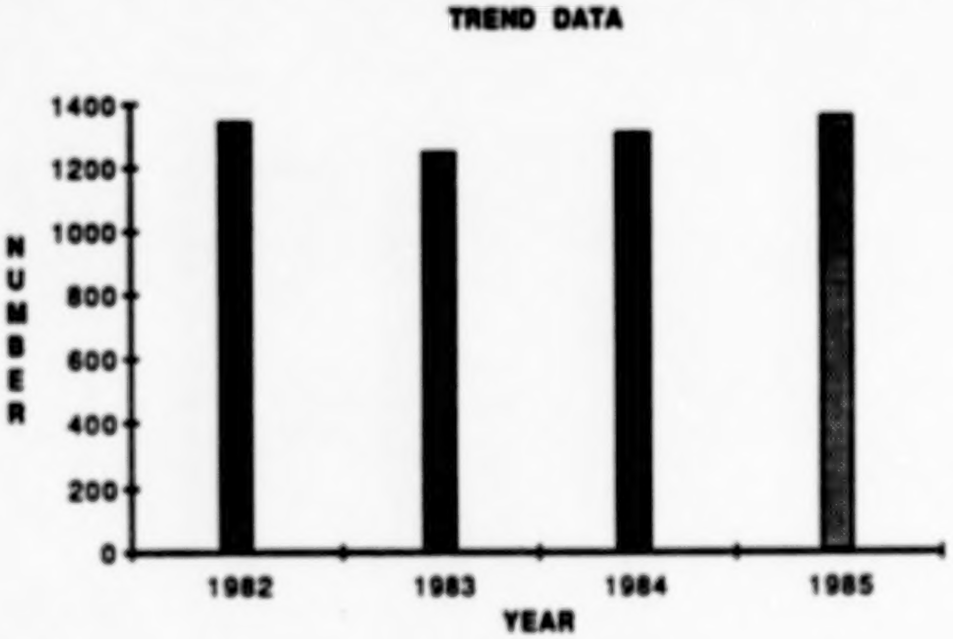


Fig. 7.14. Index counts of California sea otter range, 1982-1985.

7.6 Pup survival rates

The survival rates estimated thus far have been concerned with survival of "independent" otters, presumed to be older than 6 months of age. Survival of pups (6 months of age or younger) has been approximated by examining a large sample of observations of relative numbers of "large" and "small" pups per independent otter, collected over the years 1976-82 by Calif. Dept. of Fish and Game and U.S. Fish and Wildlife Service biologists (Fig. 7.15).

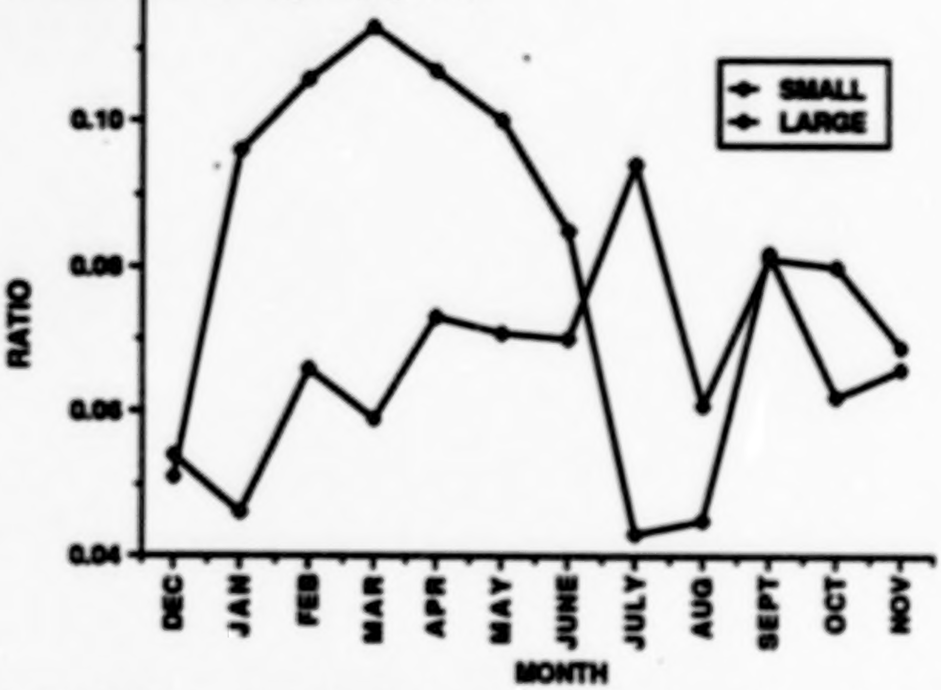


Fig. 7.15. Relative numbers of small and large sea otter pups observed in coastal study areas in California in 1976-82 by Calif. Dept. of Fish and Game and U.S. Fish and Wildlife Service biologists. Data expressed as ratios of pups per independent (free-swimming) otter.

An average relative survival rate was estimated by contrasting relative numbers of large pups (assumed to be roughly 3-6 months of age) with the peak numbers of small pups (assumed to be 0-3 months of age). That is, we considered that the survivors of the peak production of small pups (January-June) would be large pups in March to August. The results (Fig. 7.16) can be expressed as:

$$L/I = (S^*/S')(S/I)$$

That is, survival from "small" pup (S) stage to "large" pup (L) stage is denoted by S^* and survival for "independent" otters for the same period is denoted by S'. If we let the ratio of large pups per independent by $y=L/I$ and the ratio for small pups be $x=S/I$, then relative survival can be estimated as b in $y=bx$, using the simple ratio estimate of means:

$$b = y/x = 0.439/0.607 = 0.723.$$

Since the observations were taken approximately 3 months apart, one might choose to use the cube root of b as an estimate of relative survival rate. It should be emphasized that this is a relative survival rate. Transforming it to an absolute rate depends on estimating the monthly survival rate of independent otters, and thus requires survival estimates for both male and female otters from 6 months of age onwards.

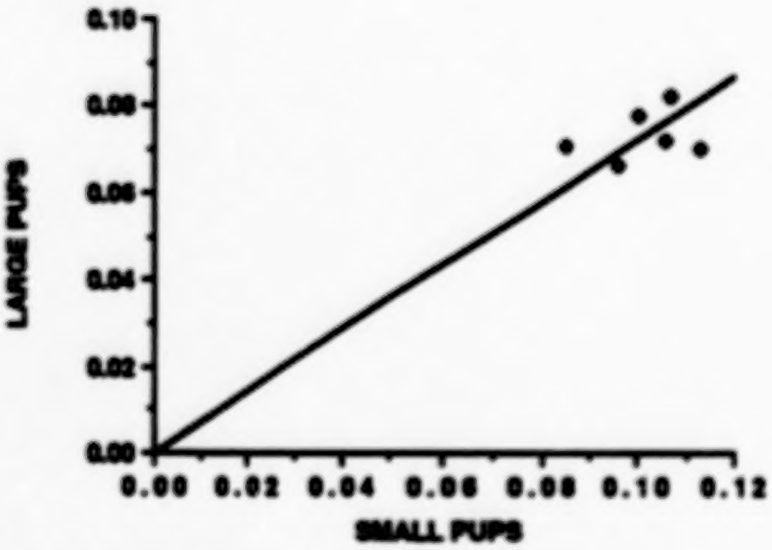


Fig. 7.16 Relative numbers of "large" pups (3-6 months of age) as a function of relative numbers of "small" pups (0-3 months of age). Numbers expressed as ratios to numbers of "independent" (free-swimming) otters.

8.0 REPRODUCTIVE RATES

Reproductive information is available from three sources. One is a set of pregnancy rates from the Aleutian Islands based on animals collected in an experimental harvest and previously described in connection with survival rates (Sec. 7.2). The second source is from the ratio of pups per independent otter observed in both California and Alaska, and the third source depends on the interval between births, estimated from resightings of tagged animals.

8.1 Reproductive cycle

Although earlier reports had indicated that sea otters give birth every second year, the recently accumulated data, from both visual sightings of tagged animals and from radiotelemetry make it clear that reproduction occurs with a periodicity much closer to one year. Because pups may be born in any month of the year, it is difficult to establish exact periods, and the telemetry data thus far suggest an average interval between births of somewhat more than 12 months. For most modelling purposes, however, we have assumed an annual cycle, with not all females reproducing in a given year, thus approximating the observed data.

It is possible that early mortality of pups may result in initiation of an estrous cycle and a new pregnancy. Winter storms may modify this situation from year to year (due to high pup mortality in some years with severe storms). Also, it is likely that there may be a longer interval between the first and second birth for an individual animal, due to the smaller size of the youngest females. Consequently, the actual average reproductive cycle is undoubtedly quite complex and may well vary from year to year and locale to locale. It will thus be very difficult to establish details of such a cycle, and sufficient data to do so may not be available for many years. Nonetheless a relatively simple cycle appears to serve satisfactorily for modelling the observed data.

In Alaska, the assumed cycle is based on a relatively high probability of giving birth (0.10) in each of 4 months (April, May, June, and July), and a low constant level (0.01) in the remaining months of the year. The underlying model assumes that the pup population is based on a year-around low level of input (0.01 pups per independent) which changes to a much higher level (0.10) in April, May, June, and July., while pups entering the population leave it 6 months later (are weaned and become "independents"). this leads to the cycle of Fig. 8.1. Pup mortality is ignored in the assumed cycle, which needs further study when various data sets become available in full detail.

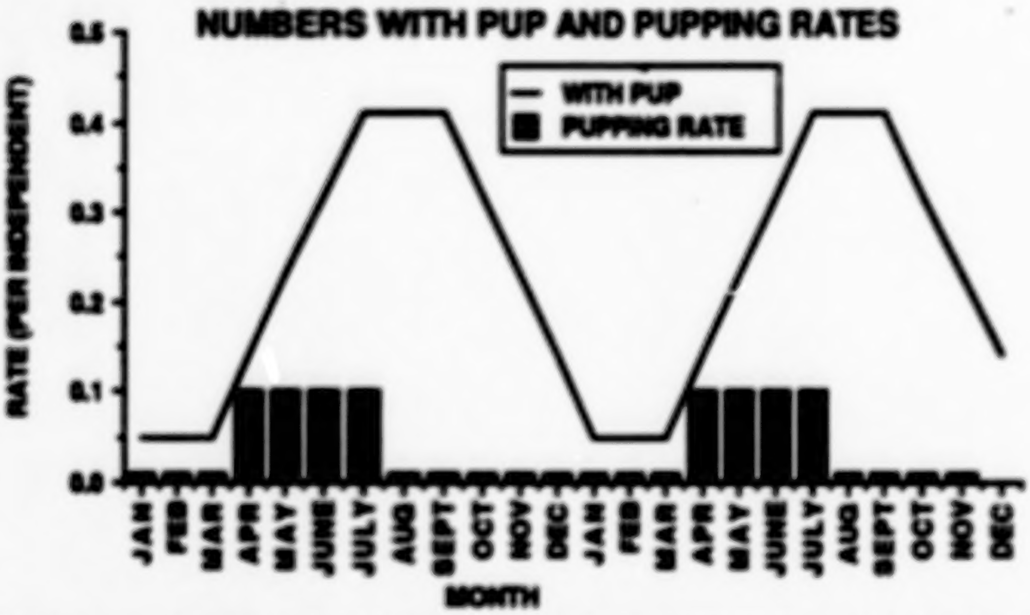


Fig. 8.1. Apparent pupping cycle of Alaskan sea otters. Pupping rates are assumed to be 0.10 for April, May, June and July, and 0.01 for all other months of the year.

If we adopt the further assumption that pregnancy lasts 6 months and the female is accompanied by a pup for the remaining 6 months of the year, the annual pupping and pregnancy cycles are as shown in Fig. 8.2.

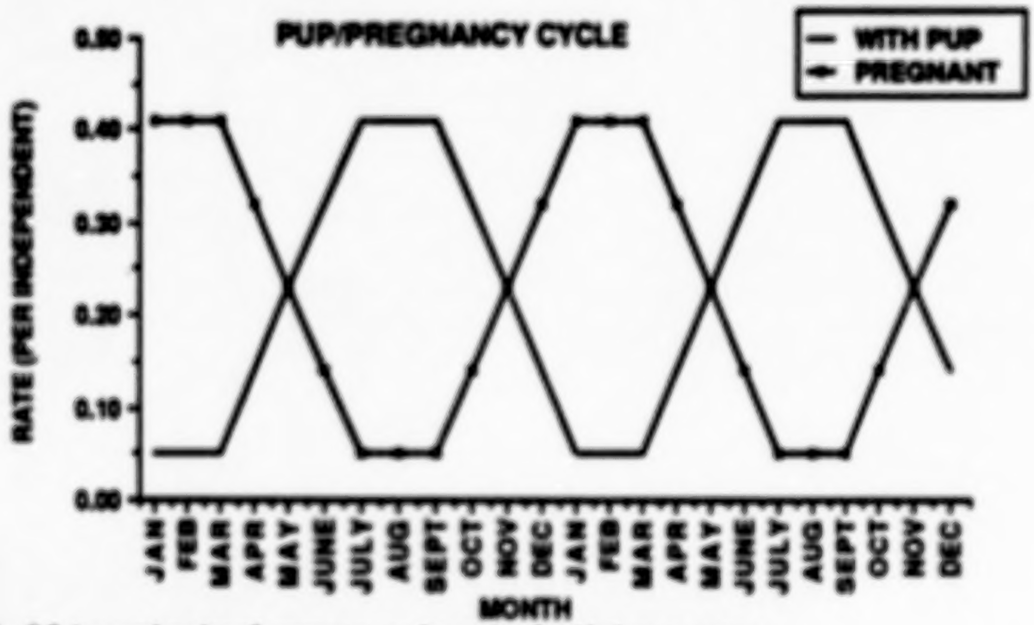


Fig. 8.2 Assumed cycles of pregnancy and pupping for Alaskan sea otters.

8.2 Pregnancy data

Schneider (unpublished report, Table 1) reported pregnancy rates for female otters taken in experimental harvests in the Aleutian Islands. He noted that the hunters deliberately avoided shooting females with pups, so that data for those months in which a high proportion of females were accompanied by pups (late summer and fall) would yield seriously biased estimates of pregnancy, due to avoidance of the non-pregnant individuals accompanied by pups. However, the early months of the year, when there are relatively few pups, should yield fairly accurate indications of pregnancy. Schneider's data (Fig. 8.3) thus seem to conform to the presumed pregnancy cycle reasonably well for the early months.

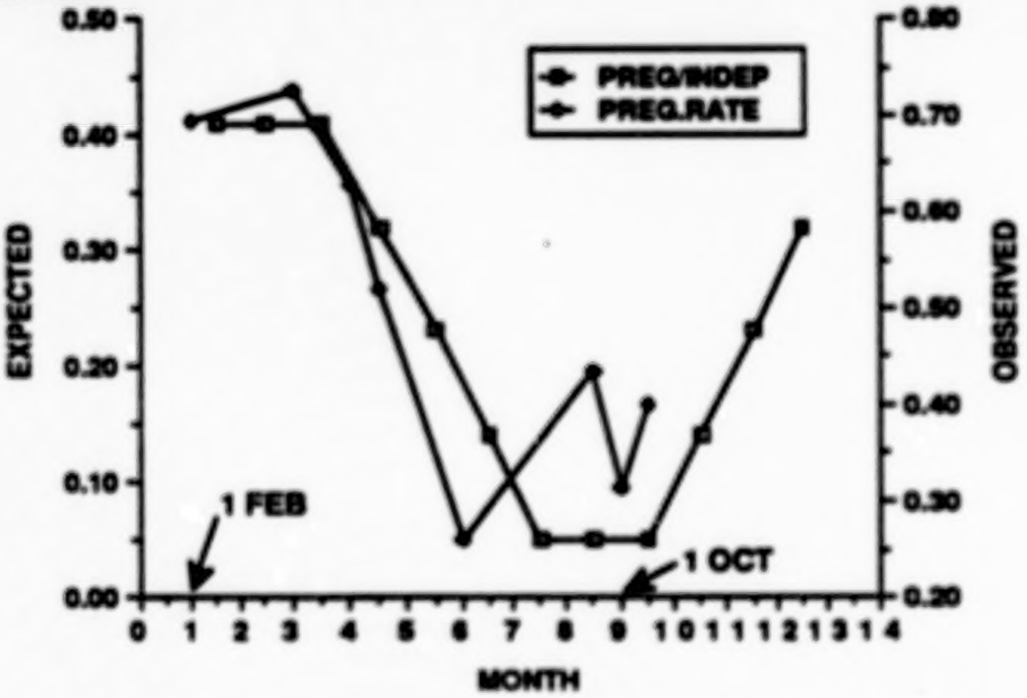


Fig. 8.3 Observed pregnancy rates in a sample of sea otters shot in the Aleutian Islands (Schneider, unpublished report, Table 1).

8.3 Observations on pupping cycle -- Alaska

Some data on the pupping cycle are available from Prince William Sound (Jameson and Johnson 1987). These are observations of pups per independent (free-swimming) otter (Fig. 8.4), and in this case represent both large and small pups. These data were used in producing the assumed cycle of Fig. 8.1, using a BASIC program, "PWS REPRO CYCLE" (Sec. 11.7).

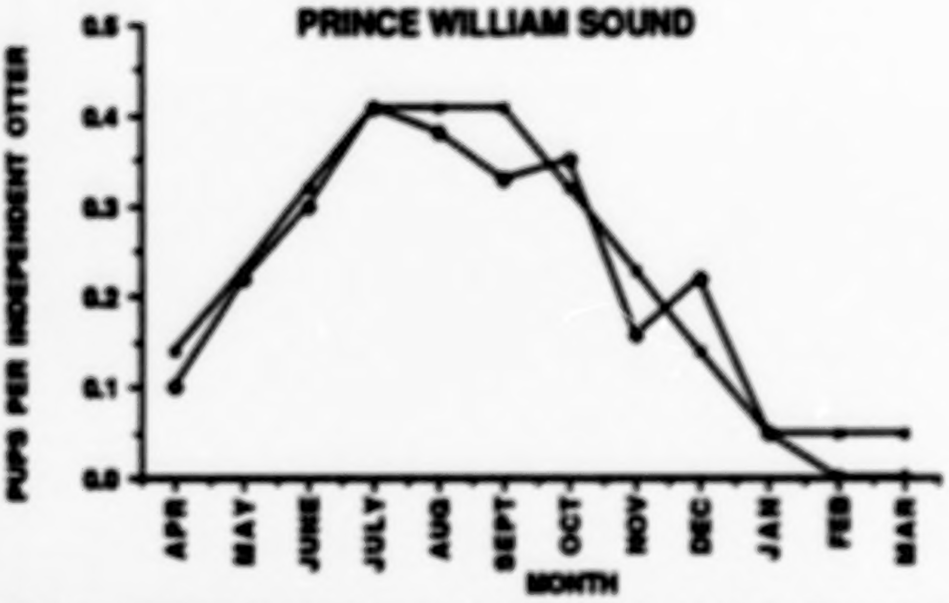


Fig. 8.4 Pups per independent otter observed in Prince William Sound, Alaska. Open symbols indicates observed, solid show expected values.

Sighting data collected by Kenyon (1969:235) on Amchitka Island (Fig. 8.5) are not nearly as well in accord with the assumed pupping cycle. However, data for the different months were collected over 5 different years.

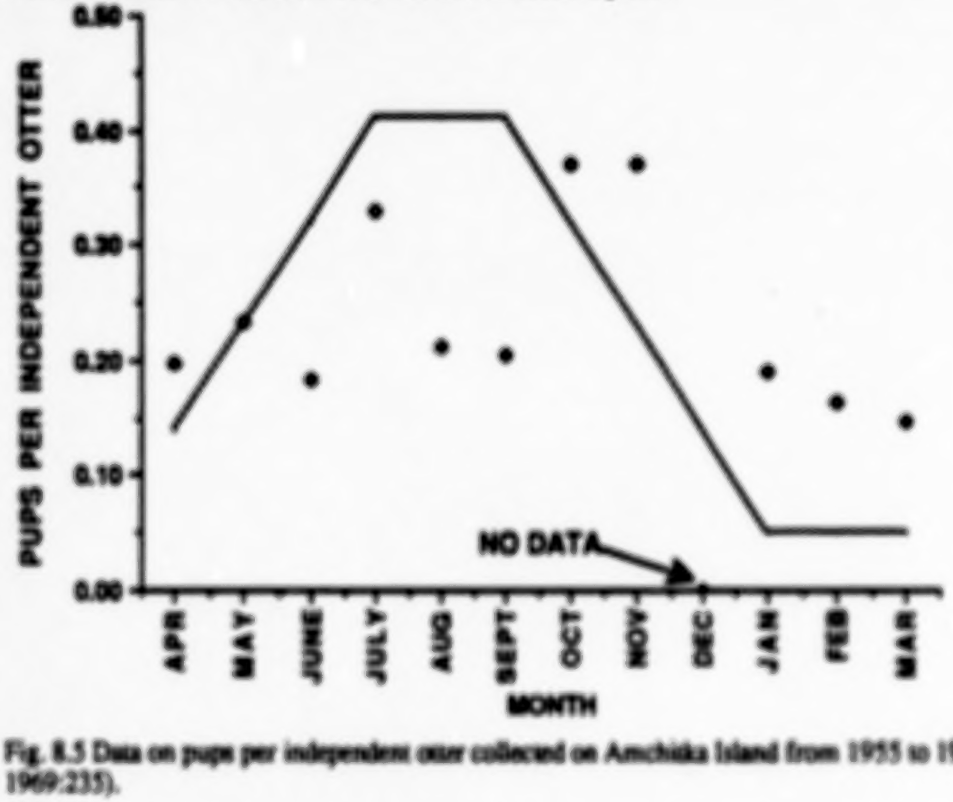


Fig. 8.5 Data on pups per independent otter collected on Amchitka Island from 1955 to 1962 (Kenyon 1969:235).

Some more recent (1987) observations (A. Johnson, personal communication, April 25, 1988) from Amchitka do, however seem in reasonable agreement with the assumed cycle, although limited to the months of October to February (Fig. 8.6). Johnson's (pers.

commun.) data were collected at Constantine Harbor and St. Makarius Bay, whereas Kenyon's data were from Constantine Harbor and vicinity.

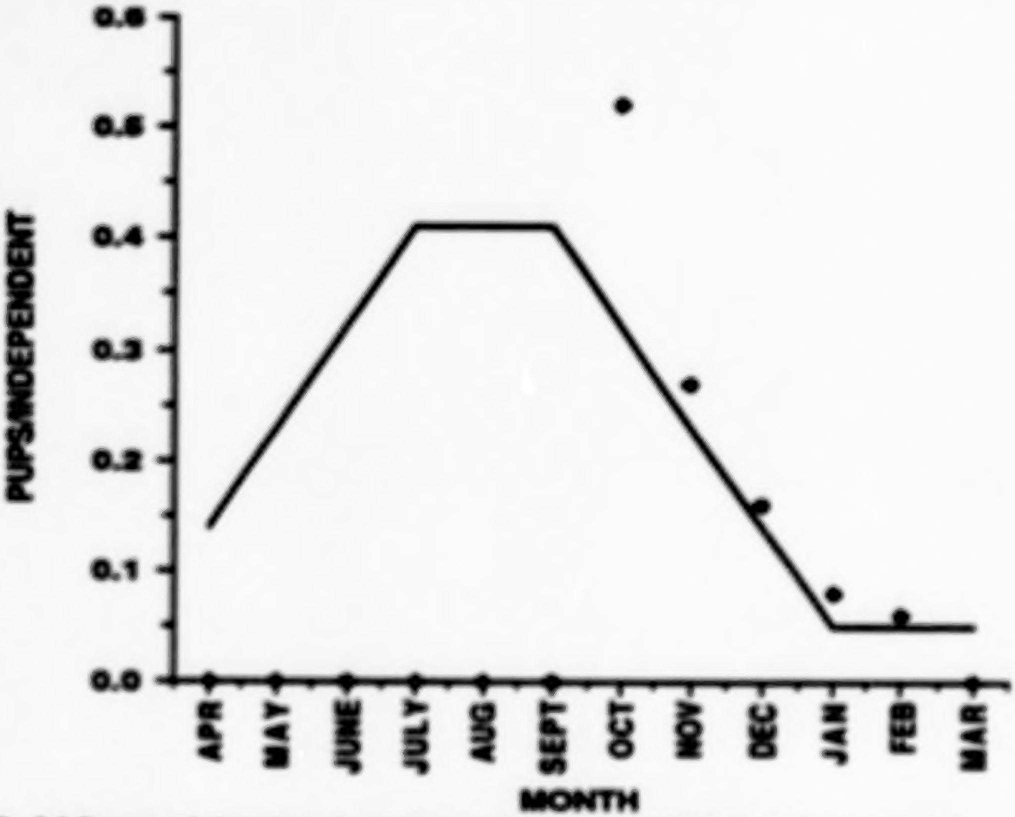


Fig. 8.6. Pups per independent observed on Amchitka Island in 1987 (A. Johnson, personal communication). Data are available for the October to February period only.

8.4. Observations on pupping cycle -- California.

Another data set is available on small pups (presumably 3 months of age or less) observed in California (Fig. 8.5). In this situation small pups seem to exhibit a fairly distinct annual cycle, while large pups have a less distinct cycle, as shown in Fig. 7.15. Also, the peak of the small-pup cycle is distinctly earlier (February-April) than the midsummer peak in Prince William Sound (Fig. 8.4). The cycle used here is based on a program ("CALIF REPRO CYCLE", Sec. 11.7) similar to that used for the Prince William Sound data, but having only a 3-months "turnover time" to represent the shift from "small" to "large" pups.

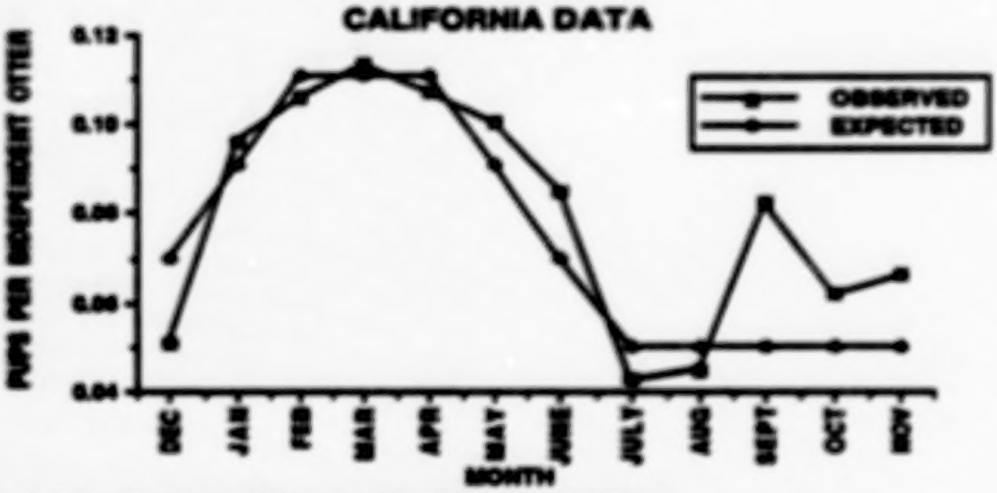


Fig. 8.7. Small pups per independent otter observed in California.

If we consider all pups (both large and small) per independent otter, the pupping cycle in California is much less distinct than that in Prince William Sound (Fig. 8.8).

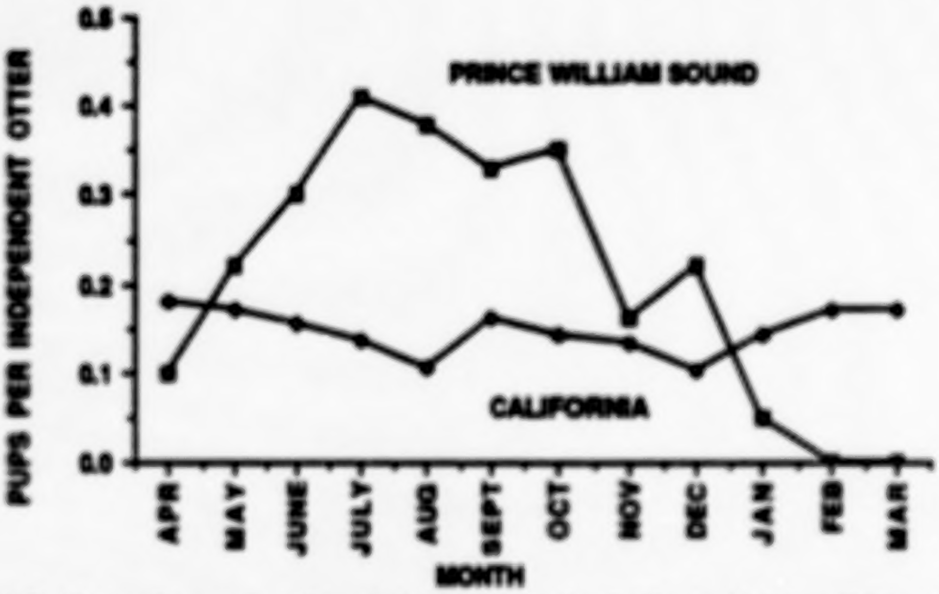


Fig. 8.8. All pups (large and small) per independent otter for California and Prince William Sound, Alaska.

8.5 Interval between births

The reproductive cycle discussed thus far is artificial in that it assumes a full cycle is completed each year. This may well be the case for the majority of individual females, but observations of tagged animals suggest that the interval between births may be variable, lasting well beyond a year for some females. The only extensive set of published data is that of Wendell et al. (1984). Since the data are based on repeated sightings of the same tagged female otters, there is uncertainty as to the exact dates on which births occur (Fig. 8.9).

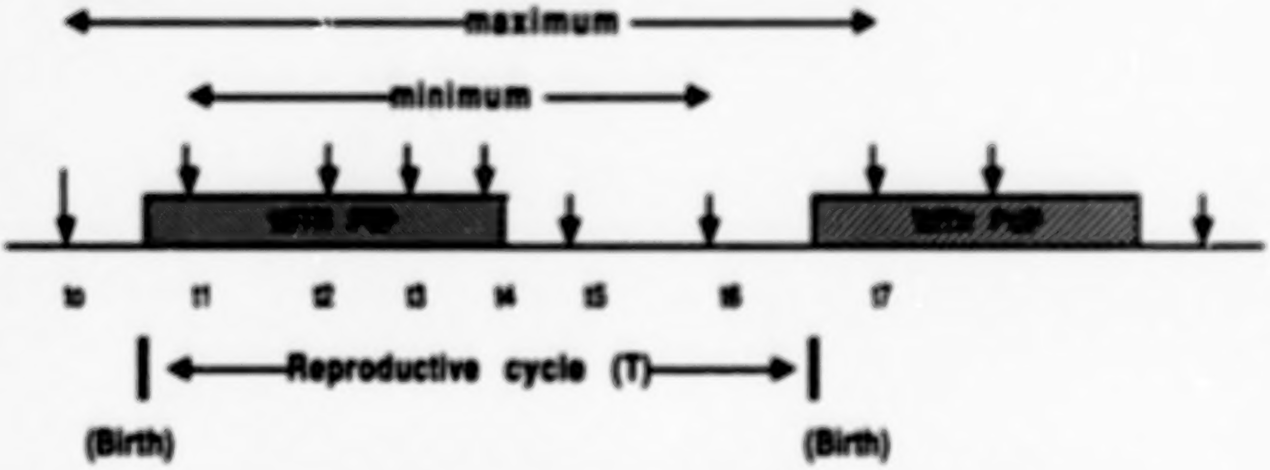


Fig. 8.9 Basis for estimating duration of reproductive cycle from observations on tagged otters. Vertical arrows denote times given female otter was identified, while shaded areas indicate actual periods when that individual was accompanied by a pup. True cycle length (birth to birth) indicated below line, while intervals for minimum and maximum estimates from observations appear above line.

Data are available on reproductive interval (Wendell et al. 1984:Table 2) for 26 otters (Fig. 8.10). Due to the uncertainty as to the exact date when births actually occured for most individuals, estimates of cycle length were calculated here as the average of maximum and minimum interval lengths (Fig. 8.9), which is the same as taking the mid-points of the intervals between last observation of females alone and first observation of female with pup. Referring to the observation times shown in Fig. 8.9, there are various combinations that might be used to estimate the reproductive cycle, i.e.:

$$T_{max} = t_7 - t_0$$
$$T_{min} = t_6 - t_1$$

and the alternative possibilities:

$$T_1 = t_7 - t_1$$
$$T_2 = t_6 - t_0$$

These are, however equivalent:

$$T_{ave} = (T_{max} + T_{min})/2 = (T_1 + T_2)/2$$

The difference between the maximum and minimum estimates represents the uncertainty as to actual duration of the true interval. Since some of these differences are quite large, we use a weighted estimate here, with the weights inversely proportional to the period of uncertainty. This gives a mean interval of 14.4 months, which is similar to the unweighted mean (also 14.4 months). The median interval is shorter being about 13.3 months.

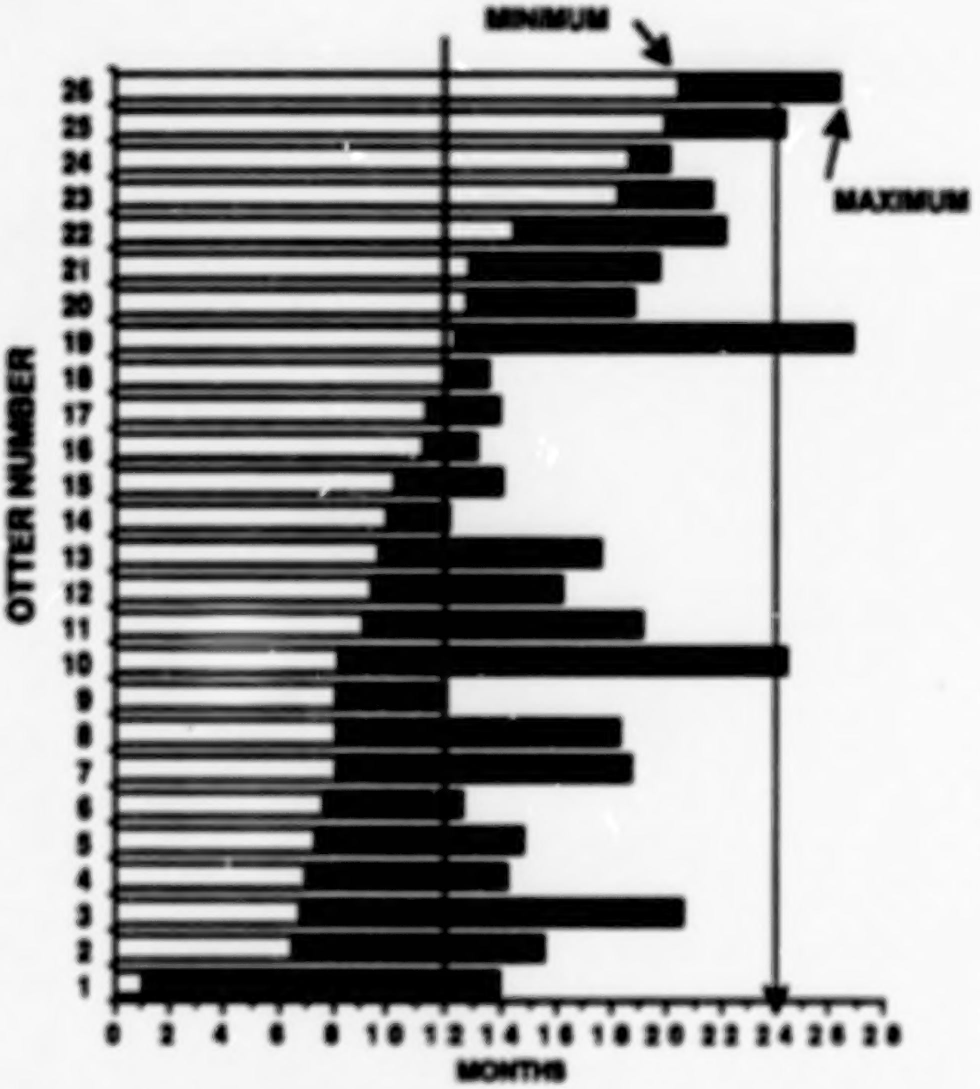


Fig. 8.10. Estimated length of reproductive cycle for tagged female sea otters in California (data of Wendell et al. 1984:Table 2). Vertical lines indicate 1 and 2 year intervals. Minimum and maximum intervals as defined in Fig. 8.9.

A plot of the relationship between the difference between maximum and minimum estimates and the actual estimates (Fig. 8.11) does not show much evidence of correlation between the two. Wendell et al. (1984:Table 1) also gave a set of data on pup dependency periods (Fig. 8.12).

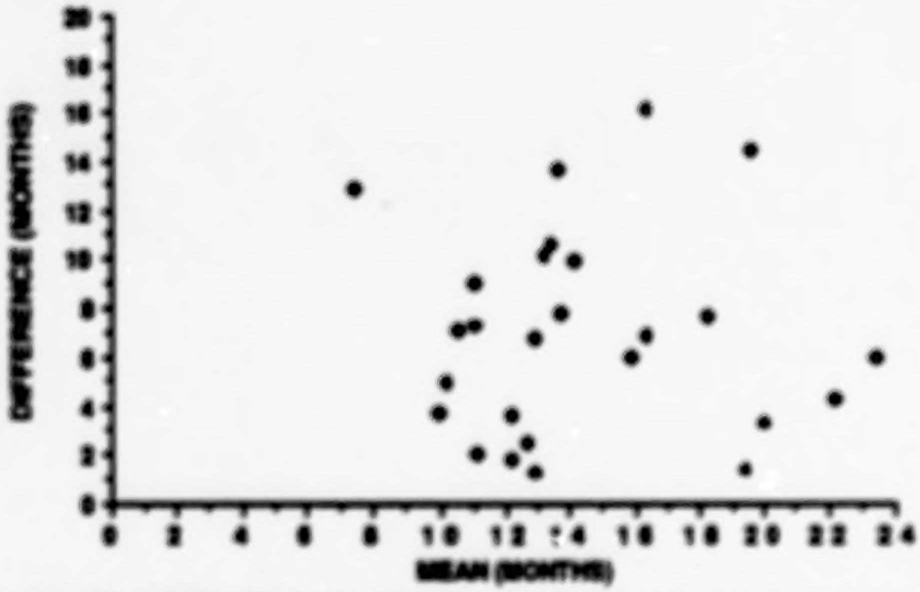


Fig. 8.11. Plot of difference between maximum and minimum estimates of reproductive interval vs. estimated interval (mean of maximum and minimum).

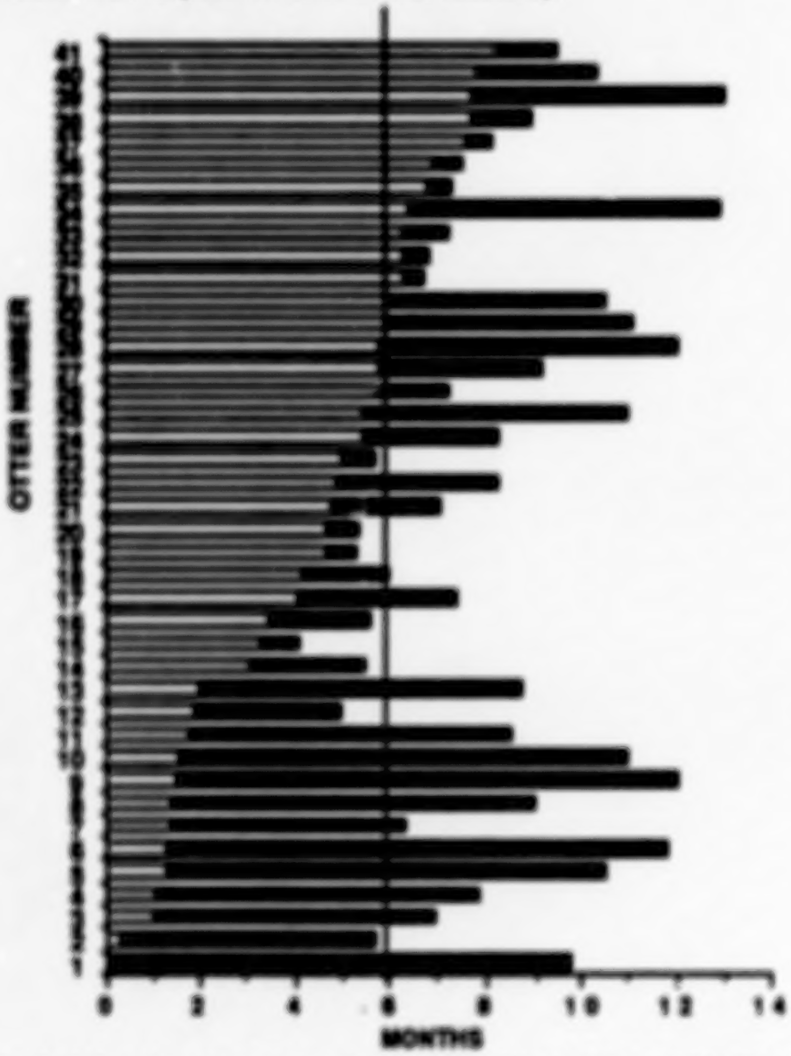


Fig. 8.12. Pup dependency intervals from data of Wendell et al. (1984:Table 1).

Estimates of an annual reproductive rate can be obtained from the reciprocals of the mean reproductive intervals. For the weighted mean, the annual rate is 12/14.41=0.83. The median gives 12/13.3=0.90. Schneider's (ibid:Table 1) Tanaga Island sample, taken in early May gave 62.8% pregnant and 13.5% postpartum, for a total of 76.3 presumably pregnant in early spring. Since further pregnancies occur throughout the rest of the year, it seems quite possible that these data will support an annual reproductive rate on the order of 0.85 to 0.90.

9.0 POPULATION MODEL

9.1 Mathematical structure of the population model.

The model used in this study is essentially a Leslie matrix model implemented without matrix mathematics. The basic model has two operating components. The first part solves the Lotka equations and establishes a stable age distribution. The Lotka equation is:

$$1 = \sum_{a}^{w} e^{-rx}\, l_x\, m_x \qquad (9.1)$$

Where r denotes population growth rate, l_x the age-specific survivorship and m_x the reproductive rates (female births per female), and a is the age of first reproduction while w is the oldest age considered. Survivorship and reproductive curves used in the model are described below (under Parameter Estimation, Sec. 9.3).

An iteritive solution of eq.(9.1) is required, and was accomplished by adding or subtracting successively smaller increments to a trial value of r until the sum was within a small range (usually about 0.0001) of unity.

The stable age structure was computed from:

$$c_x = B\, e^{-rx}\, l_x \qquad (9.2)$$

where B is calculated so that the sum of the c_x equals unity (i.e., the c_x are proportions) and thus is:

$$B = 1/\sum_{0}^{w} e^{-rx}\, l_x$$

Ages used range from weaning (age "zero") to beyond the oldest observed age. The age range starts at weaning due to the structure of the available observations, as described in Sections 7 and 8 above.

The second component of the model projects an initial population size into the future, using the survivorship and reproductive data and an intial population having the stable age distribution computed as above. This is, in effect, the Leslie matrix model, since we start out with an initial age vector based on eq. (9.2) and a total population size. Survival to the next year is computed by applying age-specific survival rates to each component (age group) of the initial vector to produce the next oldest age class in the subsequent year's vector. The first age class of the next year's vector is produced by multiplying each age class of the previous vector by an age-specific reproductive rate. Since the earliest class considered is at weaning (6 months of age), birth-rates are multiplied by survival for the first 6 months of life to yield the m_x rate used in the model. The age structure thus corresponds to "independent" otters (older than weaning age).

Outputs of the second stage of the model are thus constructed as a series of age vectors, i.e., age structures of the population at yearly intervals.

9.2 Computer formats for population model.

The initial version of the computer model ("UNIMAK") was written in the BASIC computer language, and produces the outputs described in the previous section. The program and sample outputs are included in the appendix to this report (Sec. 11.3). This initial version can easily be extended to produce the full model used here, if it is preferred to have a model in a standard language. The BASIC program can also readily be converted to FORTRAN or other standard codes if needed. However, we found that a simpler and more compact structuring of the model could be accomplished in "spreadsheet" form. A major advantage is that all of the essential parameters and outputs can easily be presented in tabular form, and major segments of the model then can be printed out on a single page.

The same result could be obtained with one of the standard computer languages. The main advantage here is that the entire model is structured in a standard, widely available format. Anyone familiar with the use of spreadsheets can thus examine and reproduce components of the model without the need to work through a computer program line by line, and does not need to consider the details of formats and output subprograms.

The present program was developed on a Microsoft MULTIPLAN spreadsheet used on a Macintosh computer, but can readily be converted to Microsoft's EXCEL (a more advanced spreadsheet program), or (with a little more difficulty) into LOTUS 1-2-3. Since both of the latter programs are available on IBM and IBM-compatible personal computers, the program can be run on most of the current generation of microcomputers. A LOTUS 1-2-3 version for IBM-compatible personal computers is described in Sec. 11.1, and was supplied to the Alaska Regional Office of MMS on floppy disks.

Apart from compatibility with other microcomputers, the main immediate advantage to utilizing one of the more advanced programs would be to introduce more complex analytical procedures for further study of the underlying data sets. MULTIPLAN will produce any of the outputs that can be supported by the presently available data on sea otter populations. Any of the Apple Macintosh computers will handle the present MULTIPLAN version. Initial model structuring was done on an older Macintosh 512, while subsequent work was accomplished on a Macintosh II.

9.3 Parameter estimates for the model.

Parameter estimates used in the model are those developed in earlier sections of this report. Since there is as yet a good deal of uncertainty as to the appropriate parameters for the population of concern, we can only present here what seem to be reasonably plausible parameters. Further field work on the sea otter population along the Alaska Peninsula will be required to obtain parameter estimates representing that population. Virtually all parameters used here were obtained from data on other sea otter populations.

Parameters for the survivorship curve for female otters were those obtained by fitting a curve to the Aleutian age structure curve (Sec. 7.4). The survivorship curve is that of eq. (7.1) reproduced here for convenience:

$$l_x = \exp[-F - Gx - D(e^{Ex} - 1)] \qquad (9.3)$$

and the values used initially are $G = -\log(S)$ with $S=0.982$, $D = 0.04526$ ($T=13$) and $E = 0.2381$ ($S_T = 4.2$). These 3 parameters gave a very good fit to the observed data (Fig. 7.3). Another set that we feel should be further explored is $S= 0.915$, $T=15$, and $S_T = 1$, as exhibited in Fig. 7.6. As noted in Sec. 7.2, the senescence parameters used in eq. (9.1) can be calculated from the equivalent forms (T, S_T) as $D = \exp(-T/S_T)$ and $E=1/S_T$. The value of F (0.0513)used was calculated from the age data on California otters (Sec. 7.4).

The reproductive curve used here is:

$$m_x = A[1 - e^{-B(x-C)}]\exp(-D(e^{Ex}-1)) \qquad (9.4)$$

Since recruitment to the modelled population occurs at weaning (6 months of age), a pregnancy rate (here assumed 90%, with half the young born being female) needs to be multiplied by survivorship to 6 months of age. A relative survival rate was obtained (Sec. 7.6) for California otters as:

$$S^*/S' = 0.723$$

where S^* represents survival from about 3 months of age to 6 months of age and S' denotes the corresponding survival of "independent" (free-swimming) otters.

Inasmuch as S' represents the average survival of both male and female otters,we used a weighted value based on the rates estimated from the only available data on both male and female otters, the California age structure data of Sec. 7.3 (male survival, $S1 = 0.723$, female survival, $S = 0.925$) and developed weights from the following equilibrium scheme:

Numbers of females surviving from annual recruitments of N females are:

$$N\,(1 + S + S^2 + S^3 + \ldots) = N/(1-S)$$

and numbers of males surviving from equal annual recruitments of N males are:

$$N\,(1 + S1 + S1^2 + S1^3 + \ldots) = N/(1- S1)$$

Hence a weighted estimate of S' is obtained from:

$$\frac{S/(1-S) + S1/(1-S1)}{1/(1-S) + 1/(1-S1)}$$

substituting the values of S (0.925) and S1 (0.723) given above gives $S' = 0.882$, with the value for 3 months being $(0.882)^{1/4} = 0.969$.
Hence $S^* = 0.723S' = 0.723(0.969) = 0.70$. Survival for 6 months then can be estimated as $(0.70)^2 = 0.49$. Consequently, $A = 0.90(0.70)/2 = 0.220$. Siniff and Ralls (1988:Ch. 2) monitored 19 pups by telemetry, and estimated survival to weaning as 0.57.

The age of first reproduction was taken as age 3, which is actually 42 months of age, and adding 6 months (the span until weaning), we have recruits to the population produced when the female is 4 years old. While relatively little information on the subject is available, we assume that full reproductive capability may not be reached at the earliest age, so we set B=2 to give maximum reproduction at age 5. The resulting l_x and m_x curves are shown in Fig. 9.1.

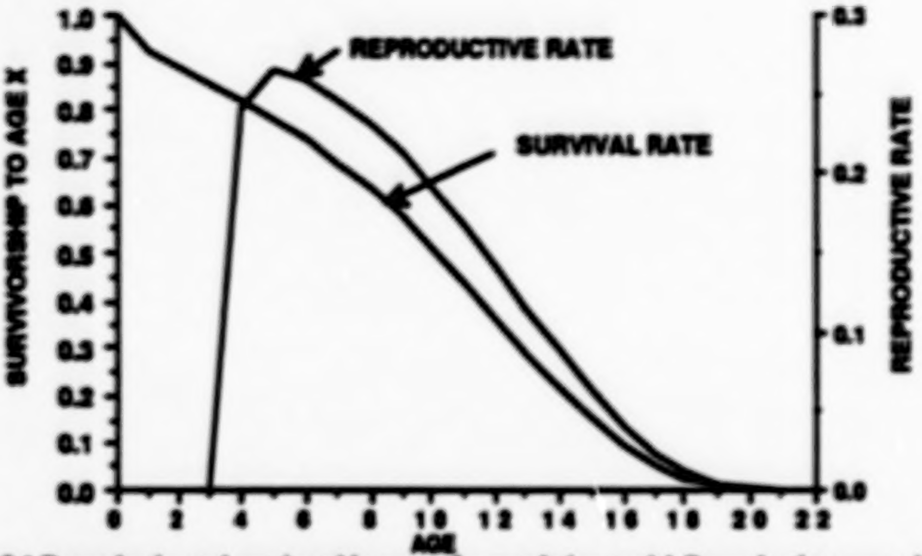


Fig. 9.1 Reproductive and survivorship curves for population model. Reproductive curve shown here is for A = 0.30 (used in later version for density dependence).

9.4 Versions of the model

Several different versions of the projection model were used to develop various features of the final model. These are all linked to the basic model (OTTERS) which sets up the stable age distribution, as described in Sec. 9.1. Any changes in the main parameters of the model (with the exception of adult male survival rates) need to be made in this basic model, which then supplies the linked projection models with necessary outputs. The various versions are shown in Fig. 9.2, and described in detail in the following sections, which also give sample outputs for each version. It should be noted that these several models are mainly important for the developmental aspects of the study, and the IBM-compatible version of Sec. 11.1 is a self-contained version of the final model developed as described here.

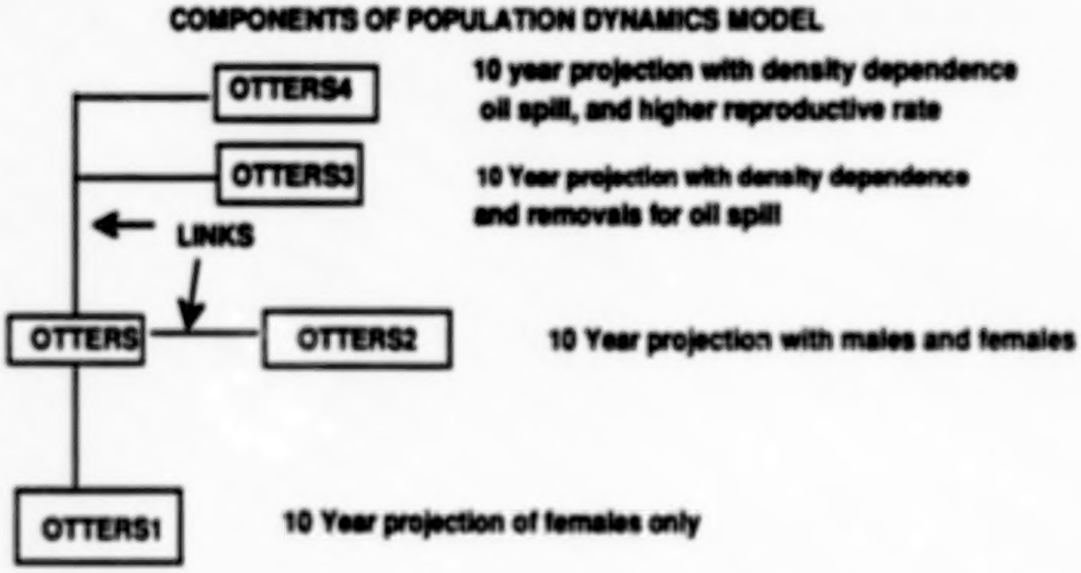

COMPONENTS OF POPULATION DYNAMICS MODEL
OTTERS4
10 year projection with density dependence
oil spill, and higher reproductive rate
OTTERS3
10 Year projection with density dependence
and removals for oil spill
LINKS
OTTERS
OTTERS2
10 Year projection with males and females
OTTERS1
10 Year projection of females only

Fig. 9.2. Components of the population models used in this study. The basic model is "OTTERS" which sets up a stable age distribution for each of the projection models shown linked to it.

9.5 Basic model

As noted above, the basic model ("OTTERS") serves to generate the stable age distribution from any given set of parameters for the l_x and m_x curves previously described. An example appears as Table 11.1 in Sec. 11.9.

9.6 A projection model

The model OTTERS1 was used in development of the other models, and serves mainly to show the concurrence of the spreadsheet models with the BASIC program model initially developed as discussed in Sec. 9.2. Output from this model is shown with that from the BASIC model in the appendix (Sec. 11.3). It is essentially the same as the female component of the model described in Sec. 9.7.

9.7 A model with two sexes.

A projection model with two sexes ("OTTERS2") is illustrated in Table 11.2. Calculations needed to partition the two sexes and set up the male table proceed as follows. An essential parameter is a male survival rate, which is available only from age structure data for California as discussed in Sec. 7.3. We thus have to assume the male survival rate is proportional to that of females in the same ratio in Alaska as in California, and calculate the needed male survival rates by using the ratio of rates obtained in California (i.e., S1 the male survival rate, is calculated by multiplying female rate (S) by 0.723/0.925=0.782, the ratio of the rates estimated in California). The adult male survival rate corresponding to the selected female rate is then used with the other parameters developed earlier (i.e., early survivorship is assumed the same in males and females) in eq.(9.3) to develop the l_x curve for males. Since the female parameters govern the rate of increase of the population (calculated in OTTERS, Table 11.1), we thus have the data to calculate a stable age structure (c_x) for males from eqn (9.2).

Given the proportional age structures for males and females, as shown in Fig. 9.3, we can then relate the fractions of males and females recruited (C^* for females, C_0 for males; highlighted in Fig. 9.3) by using sex ratio (R) at birth, which is here assumed to be unity (R=1). With this relationship between the two proportional age structures, the total population size (N_T) can be partitioned into males (N_m) and females (N_f). This then gives an initial age vector for males and the abundance of males beyond the initial age class is calculated by using the survival rates. The first entry in each age vector is identical to that for females, since the sex ratio at birth is assumed equal (and survivorship for the first 6 months is also assumed equal). We thus have complete age structures for males and females. The approach can be summarized as follows:

Total population (N_T) = number of males (N_m) + number of females (N_f)

Sex ratio at recruitment = R (here assumed to be 1.0)

Number of male recruits = $C_0 N_m$ = R (number of female recruits)
= $R(C^* N_f)$

Solving for N_m:

$$N_m = \frac{RC^*N_T}{RC^* + C_0}$$

with C_0 and C^* being proportions of male and female recruits (age class zero) in the stable age distributions of Fig. 9.3.

As is evident from the totals at the bottom of Table 11.2(Sec. 11.9), the projection reflects the result forecast by the initial program (OTTERS), i.e., that the population size is virtually constant. The small fluctuations in the totals reflect rounding errors in calculations. If fractions of individuals are used in the calculations, the rates of change calculated from such a projection will reflect the value of the rate of increase calculated from the Lotka equation to the 3rd or 4th decimal place. In reality, the parameters developed earlier for the program OTTERS do not quite yield a constant population level. It was necessary to increase the reproductive rate (A) slightly to achieve a balance. Thus it is shown as 0.226 in Table 11.1, whereas the calculations gave 0.220 (Sec. 9.3) above.

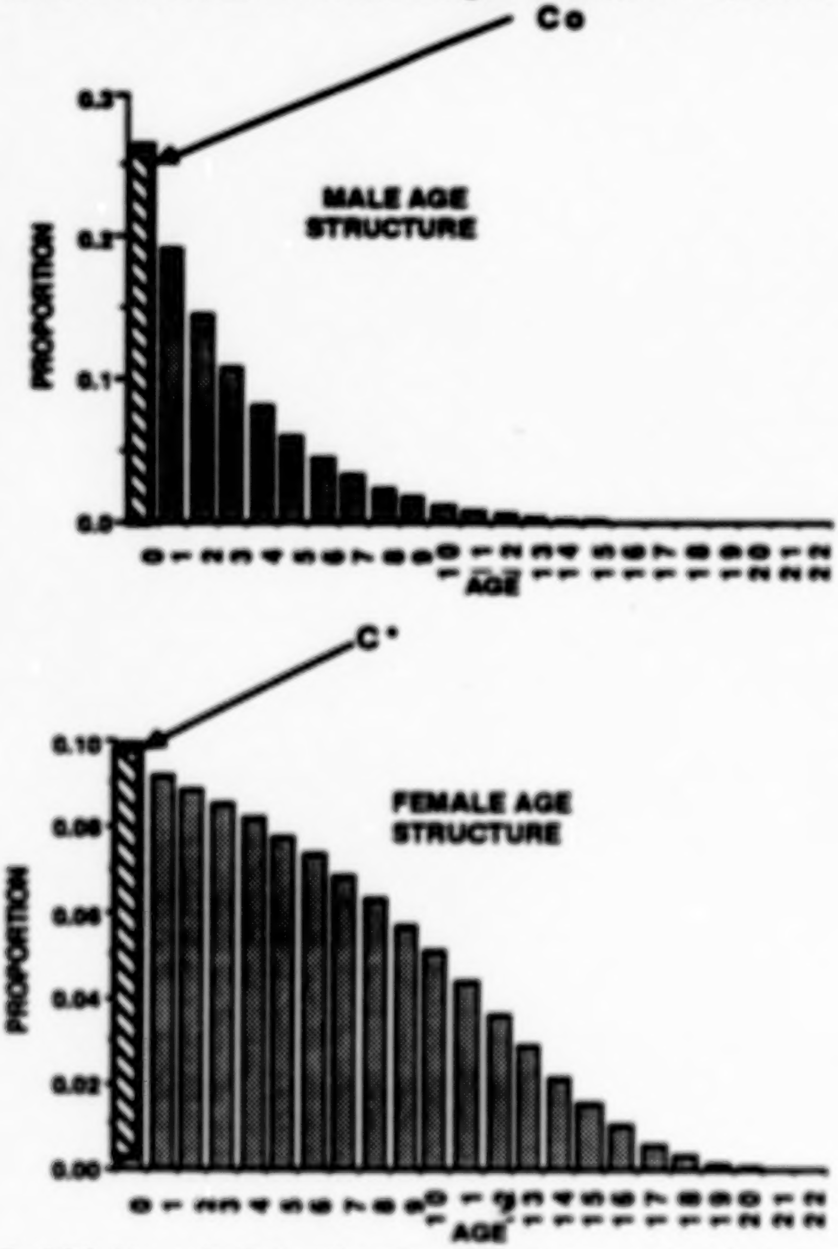


Fig. 9.3 Stable age distributions for male and female otters used to calculate male age structure from data on females.

9.8 Population model with density dependence

The parameter estimates developed above (Sec. 9.3) yield a population that is essentially constant in size. If total population size is reduced, the modelled population would remain at the reduced level, apart from some minor fluctuations that might result if the removals yield an age structure different from the stable age distribution of eq.(9.2). A realistic model for oil spill effects then has to incorporate some sort of density dependence function that will tend to return the population to its former level.

Unfortunately, very little is known about density dependence in general, and even less about density dependence in sea otters. Evidence for other species (Eberhardt 1977) suggests that density dependence is likely to operate first on early survival, and then perhaps on reproductive rate. Since the model used here pertains to otters older than 6 months of age, both effects would operate to reduce numbers in the first age classes of Table 11.2 (Sec. 11.9), so a density dependence function has been introduced at that level. One other preliminary needs to be considered first, however.

If we assume the present population is constant due to a density dependence effect, then the population will return to that level after a removal due to a simulated oil spill only if the basic population parameters are such that a positive rate of increase would be generated. The parameters we have estimated are approximately those for a constant population, as would be expected at "carrying capacity". Hence, we need to assume a higher potential rate before introducing density dependence. For illustrative purposes here we have thus set A = 0.30 in OTTERS, giving the result shown in Table 11.3, with an annual rate of increase of about 4% per year.

Density dependence was introduced by using the generalized logistic function variously proposed for use with marine mammals (e.g., by the International Whaling Commission's regulatory process):

$$p = 1 - (N/K)^z \qquad (9.5)$$

where N is current population level, K is asymptotic or "carrying capacity" level, and z is an arbitrary constant greater than unity. Fig. 9.4 shows the effect of some values of z:

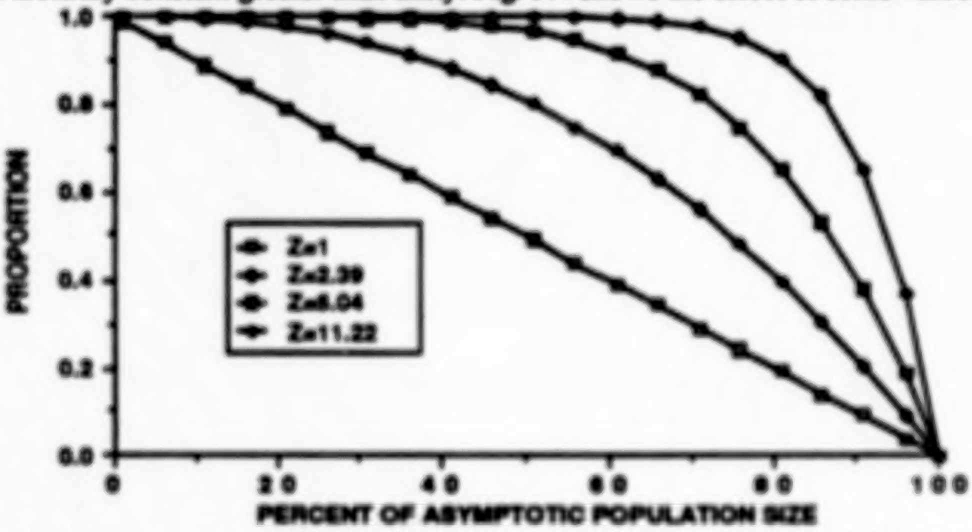


Fig. 9.4 Magnitude of the expression given by eq.(9.6) for various values of N/K. The lowest line shown is that for the ordinary logistic function (z = 1). As z increases, density dependence begins to take effect only as the population becomes relatively close to its asymptotic value (100%).

The density dependence function is introduced into the population model (OTTERS3) as illustrated in Table 11.4 (Sec. 11.9). Recruitment into the first age class of Table 11.2 is now reduced in accord with eq.(9.5). From the form of eq. (9.5), it can be seen that if population size (N) exceeds carrying capacity, the multiplier would become negative, an unrealistic outcome. Hence the spreadsheet contains an "IF statement" that sets the multiplier equal to zero whenever N exceeds K.

One further feature of OTTERS3 is the introduction of a mechanism to represent the effects of an oil spill, by way of a vector of proportional multipliers in Table 11.4. These multipliers operate between year 1 and year 2, i.e., N1 (females) is reduced by multiplication by the vector of column 26, giving a reduced population going into the next year. The same effect operates on males (after N1M, yielding a lowered population going into the next year, as with females).

A problem with the present approach is that increasing A in OTTERS to produce recruitment rates capable of inducing recovery after a simulated oil spill generates a stable age structure appropriate to an increasing (rather than a constant) population. Using this structure in a population presumably at carrying capacity leads to some perturbations in age structure as is evident in the age vectors of Table 11.4(Sec. 11.9). An alternative is to continue to use the survival rates and age structure established for a population at a constant level (Table 11.1) but to combine these with reproductive rates giving a positive rate of increase, as in Table 11.3 We thus removed the linkage to the reproductive rates in OTTERS, and calculated reproductive rates directly in a new version of the projection model (OTTERS4), so the necessary parameters now appear at the top left of Table 11.5, which is otherwise structured the same as OTTERS3. This removes the perturbation in female age structures evident in Table 11.4.

Fig. 9.5 (produced from Table 11.5) shows the population trend induced by an oil spill removing about 20% of the population after the first year. Further manipulation of the models needs to be considered after Minerals Management Service staff determine the kinds of simulations deemed necessary for their purposes, and should also depend on any further information obtained on current parameters and status of the sea otter populations in the area of concern.

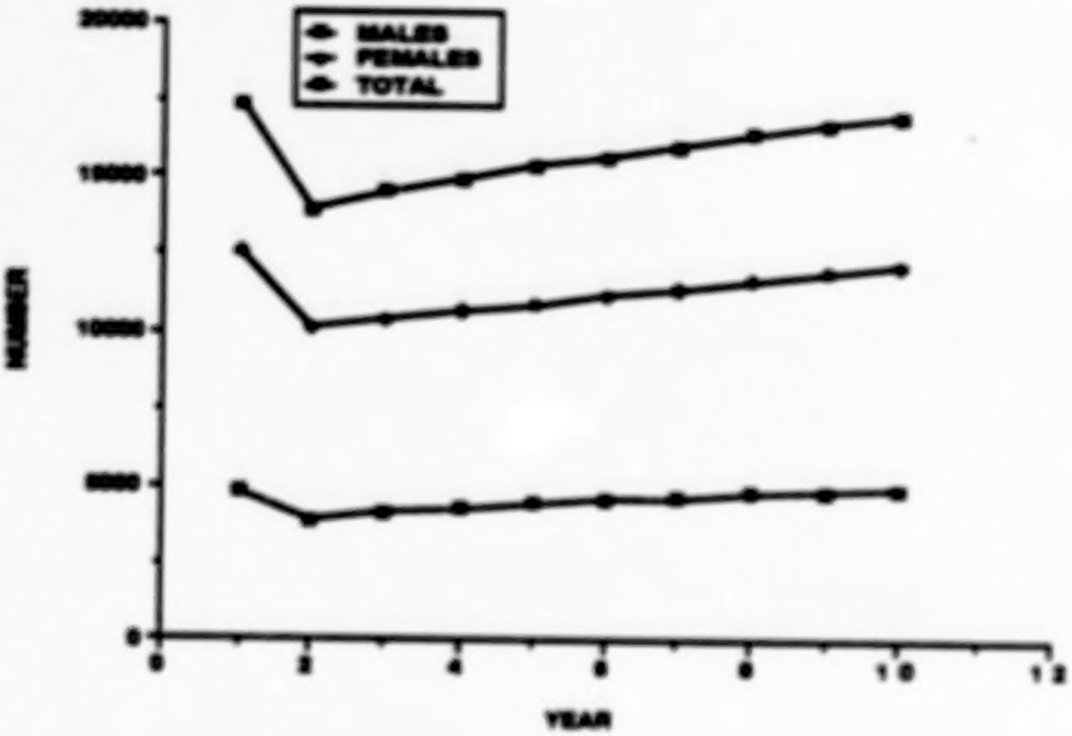


Fig. 9.5 Population trend of modelled sea otter population after a simulated oil spill.

10.0 PARAMETER ASSESSMENT AND DATA NEEDED

This section attempts to assess the utility of various parameter estimates and considers data needed for a satisfactory model of sea otter populations. In the logical sequence of the conceptual approach proposed in Fig. 5.2, the present section is out of order. That is, an effort to test assumptions and hypotheses about the data conceptually should be made before models are structured and assembled. However, several of the potentially useful data sets have not been available in detail as yet. Consequently, a continuing effort at modelling sea otter populations is needed, and this section describes some useful approaches and data needs.

10.1 The bootstrap approach to assessing data sets

Any effort to intercompare the several sources of information on sea otter population dynamics used here requires a way to assess both variability of sources and their overall compatibility. There is, for example, no standard statistical technique for computing a variance estimate for the rate of change (λ or e^r) in eq. (9.1), the Lotka equation. However, a recently developed method, "bootstrapping"(Efron 1982, Efron and Gong 1983)), does provide a way to directly and graphically exhibit the inherent variability in both individual sources and for their combined outcome .

To avoid some of the complications inherent in the structure of eqs. (9.3) and (9.4) we used a simplification (Eberhardt et al. 1982) that permits expressing eq. (9.1) by a reduced number of parameters:

$$1 = \lambda^{-a}\, l_m\, s^{a-m}\, f \left[\frac{1 - (s/\lambda)^{w-a+1}}{1 - s/\lambda}\right] \qquad (10.1)$$

The simplification leading to this equation largely amounts to using truncation to eliminate the parameters representing senescence, and reducing m_x (eq.(9.4)) to a single parameter, f. We thus assume no otters survive beyond age 15 (w), and that females begin to reproduce at this rate at age 4 (a). Early survival is represented by l_m, and a constant survival rate is assumed beyond age m(used initially as m=3). A finite rate of increase is assumed, i.e., $\lambda = e^r$ in eq. (9.1).

10.2 Bootstrapping the telemetry data

For an initial demonstration of the bootstrapping approach, we use the telemetry data of Siniff and Ralls (1988:Ch. 2). Four components are used to calculate eq. (10.1). Adult female survival (s) was calculated by the method used by Heisey and Fuller (1985), which amounts simply to the usual binomial calculation, where the number surviving equals 1 - p, where p is the proportion dying in the interval considered. However, Heisey and Fuller (1985) assume that each day of observation by telemetry amounts to an independent observation, thus accumulating a very large number of "transmitter days" in the denominator of the survival estimate. Hence, for example, Siniff and Ralls (1988:Ch. 2) reported some 7560 transmitter-days of observation on 16 adult female sea otters, during which there were 2 deaths. Consequently a daily rate of mortality is calculated as $p = 2/7560$, and its complement raised to 365 days to estimate an annual survival rate:

$$\text{annual survival} = (1 - 2/7560)^{365} = 0.908.$$

It seems very doubtful that one can safely use the usual binomial variance here, $V(p) = pq/n$, with $n = 7{,}560$. Instead, we use the bootstrapping approach, which amounts simply to taking repeated random samples of the observations of the 16 individual adult female sea otters with replacement, and constructing the survival estimate above independently for each set of sample observations. That is, we list the "population" of 16 observations of individual otters with each represented by a serial number, the number of transmitter-days, and survival (1=survived, 0=died), and take, say, 300 random samples of 16 observations each (with replacement, so that each individual has the same chance of being drawn in each selection) and calculate survival for each such set of 16 observations by the equation given above. The outcomes of this "resampling" process can be shown as frequency distributions as in the various illustrations given below, yielding a notion of the variability of individual components from the spread of the frequency distributions.

Survival to the "age of maturity", l_m, was calculated as survival to age 3, being the product of pup survival (sample of 18 pups) and the survival of juveniles (10 females and 5 males combined), so that we have, for eq.(10.1): $l_m = s_{pups} s_{juv}^{2.5}$. The reproductive rate (f) is based on a sample of 10 reproductive intervals, 5 reported by Siniff and Ralls (1988: Ch. 2) and 5 of comparable accuracy taken from the data of Wendell et al. (1984).

The four components used for eq. (10.1) were each independently randomly sampled with replacement 300 times (with the individual sample sizes corresponding to the observed data, i.e., 16, 18, 15, and 10) and the outcomes of each written to computer files. These 4 files were then used to calculate 300 values of λ from eq. (10.1), and the outcomes are exhibited in Fig. 10.1. The various operations were carried out by simple computer programs listed in Sec. 11.8. For the present example, programs BOOT, BOOT3A, BOOT4, AND BOOT5 were used to generate data used in BOOTS to calculate the values of λ summarized in Fig. 10.1.

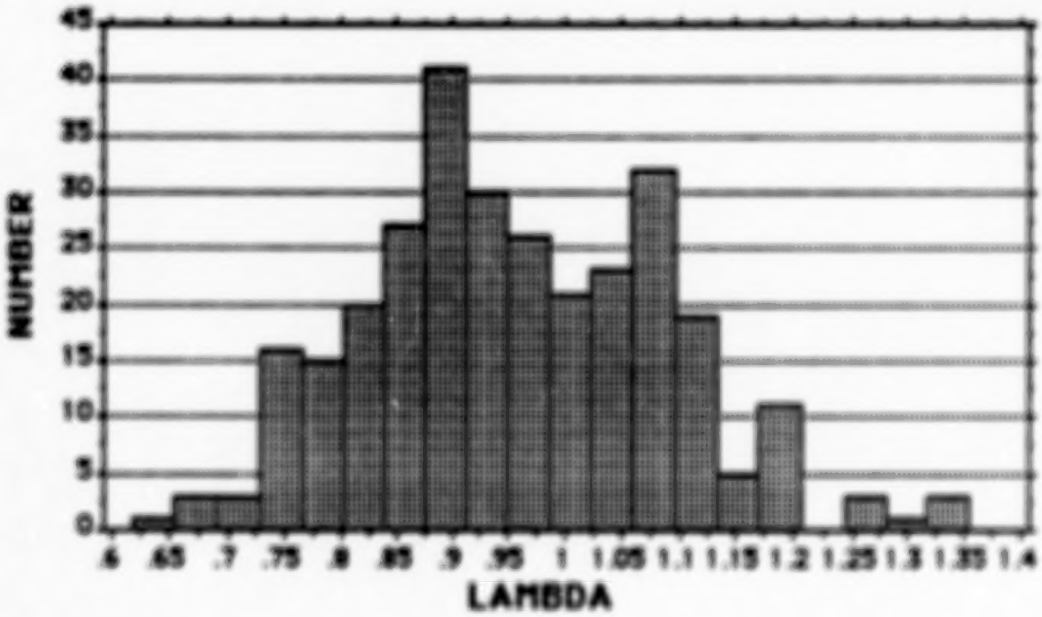


Fig. 10.1 Frequency distribution of 300 values of lambda generated from telemetry data and used in eq. 10.1.

10.3 Increasing sample sizes for calculations

From the spread of the estimates of λ in Fig. 10.1, it is clear that the sample sizes for the telemetry data are inadequate to yield much information about the rate of increase. We thus need to consider any information providing a narrower spread of results, as well as considering the evidence bearing on accuracy of the individual samples. From independent data on population trend (Figs. 7.13 and 7.14), we know that the California population was at a nearly constant (stationary) level for many years, whereas the average value of l in the data of Fig. 10.1 is about 0.95, thus indicating a population decreasing at about 5% per year.

One prospect for reducing variability is to use adult female survival rates based on the age data described in Section 7.3. Using the data on females aged 4 to 12, shown in Fig. 10.2, and carrying out the bootstrap procedure (program BOOTS in Sec. 11.8) yields an appreciably narrower spread for the survival estimates, as shown in Fig. 10.3, which compares the survival estimates from telemetry data with those using age structure data.

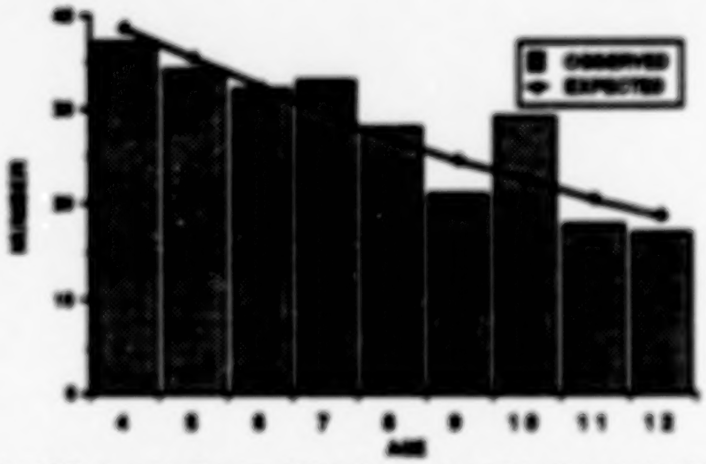


Fig. 10.2. Age distribution of female otters found dead along the California coast, with expected values based on survival estimate from the Chapman-Robson method.

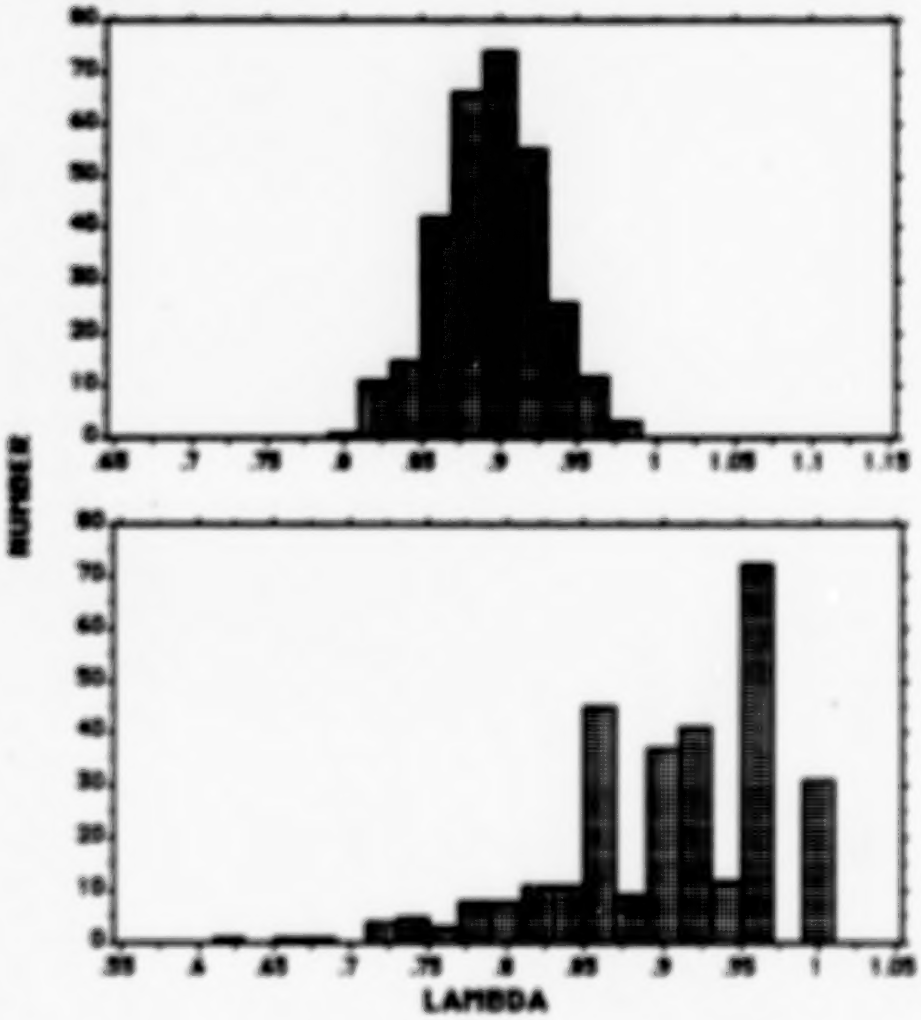


Fig. 10.3 Survival estimates from telemetry data (lower) compared with those from age distribution data (upper panel).

A similar result can be obtained by using the full set of reproductive interval estimates of Wendell et al. (1984), discussed in Section 8.5, and again using a weighted estimate. This gives the narrower spread of outcomes shown in Fig. 10.4.

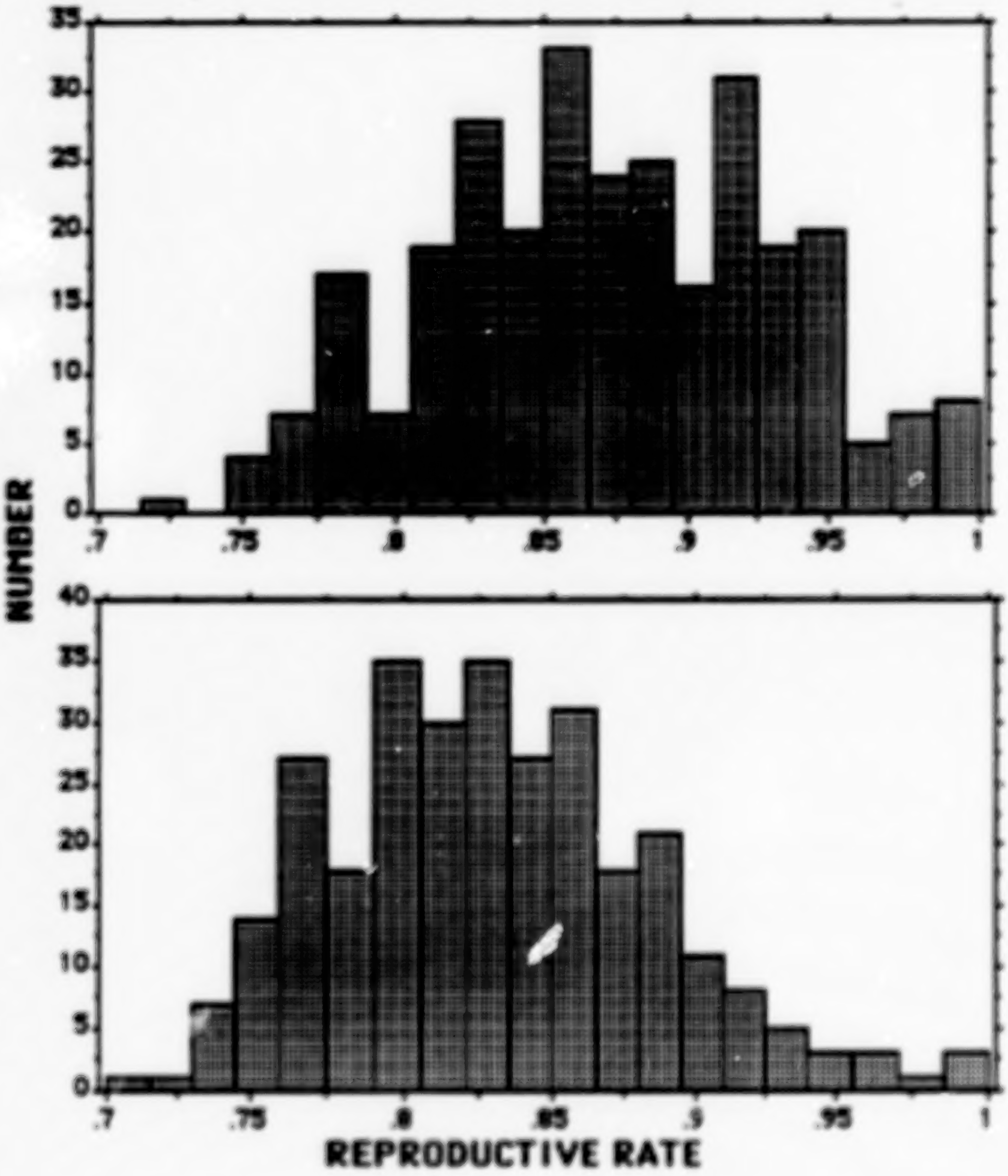


Fig. 10.4. Reproductive rates from small sample (upper panel) based on 5 observations from telemetry data and 5 with similar accuracy from Wendell et al.(1984) compared to distribution from full sample of Wendell et al. (lower panel).

The sample for pup survival can be enlarged by incorporating data reported by other investigators. Jameson and Johnson (1987) reported that 16 of 42 pups observed with adult females disappeared before 5 months of age, and were thus assumed to have died. Wendell et al. (1984:97) reported that 5 of 12 tagged pups were known to have successfully weaned. This then gives an overall pup survival rate of 40/72 = 0.556, which was used in BOOT5A to provide an enlarged data set for pups. The data on otters found dead can be used as described in Sec. 7.4 to estimate early survival. This is accomplished in program BOOT2, which samples the age data of females aged 1-12, and estimates the early survival coefficient as in Sec. 7.4. These data were then combined in program BOOTS2 to provide a new set of estimates of lambda, as shown in Fig. 10.5.

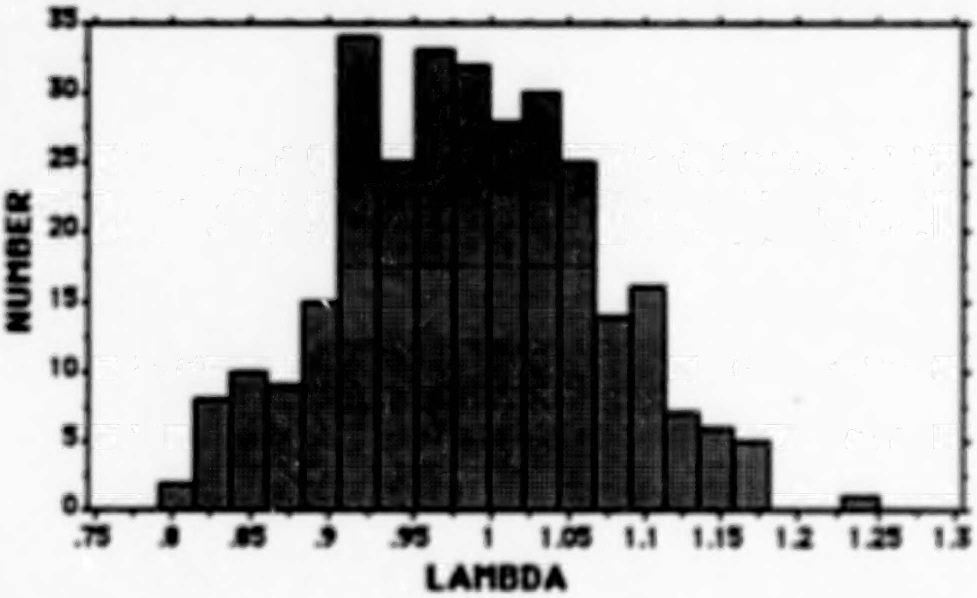


Fig. 10.5. Estimates of λ obtained with the enlarged data samples described above, and using program BOOTS2.

The average value of λ obtained from 300 bootstrap samples is 0.987, while the median is about 0.985. This data set thus agrees fairly well with the count data, i.e., suggests the population is nearly constant. As is evident in comparison with Fig. 10.2, there is an appreciably smaller spread in the estimates.

10.4 An alternative estimate of early survival

The estimates of early survival from telemetry data were based on pup survival and juvenile survival rates. For a larger sample, we used additional observations on pup survival and an estimate of early survival from age structure data calculated as in Sec. 7.4, but using adult female survival based on data from ages 4-12. The calculation is:

$$p = \frac{1 - e^{-F-2G}}{1 - e^{-F-12G}} = \frac{1 - S_0 S^2}{1 - S_0 S^{12}} = \frac{59}{178} = 0.3315$$

giving $S_0 = 0.925$.

As an alternative approach, we can used the data of Ames et al. (1985), who reported 183 "immatures" in 708 carcasses of sea otters older than pups picked up on California beaches. If we assume subadults to be 1 and 2 years of age, then their proportion in the population of otters older than pups will be: $p = 1 - e^{F-2G} = 1 - S_0 S^2 = 183/708 = 0.2585$. In this case, the denominator is unity, since all otters (older than pups) are considered, whereas before we considered only otters through age 12, due to the likely under-representation of the oldest otters in the sample aged discussed in Sec. 7.3. Using the estimate of adult survival of 0.915 (based on ages 4-12) gives $S_0 = 0.886$. Using this data in BOOTS2A (modified from BOOTS2 to incorporate the above calculation on bootstrapped data on proportions of subadults calculated in BOOT6) gives values of λ shown in Fig. 10.6, which has a mean value of 0.980 and a median of 0.979, a little less than in Fig. 10.5. Also, Siniff and Ralls (1987:Ch. 6) found this age classification ("immatures") to be principally one-year olds, but also found some 1 and 2 year olds in the next older class ("subadults").

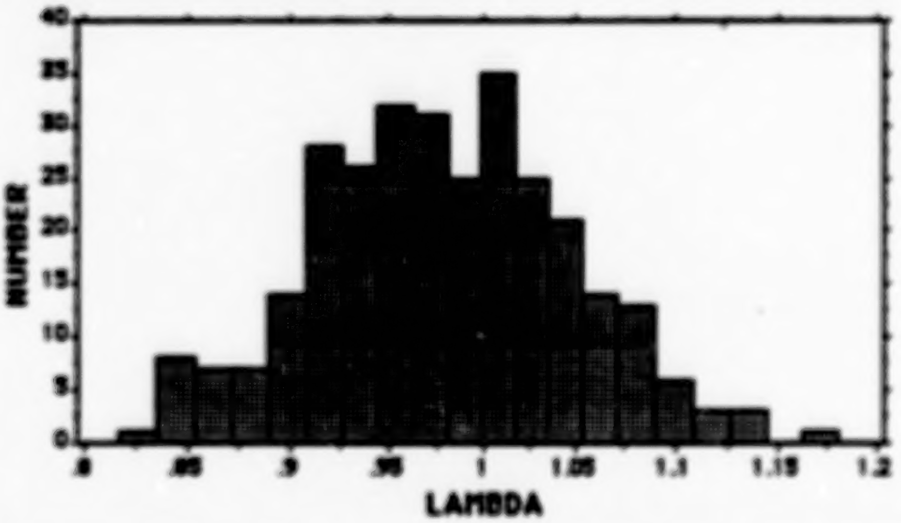


Fig. 10.6. Estimates of λ using proportion of "immatures" reported by Ames et al. (1985) to estimate early survival rate.

10.5 Population growth rates for Alaskan sea otters

Many existing sea otter populations may well be at more or less constant population levels, as with the California population. In the event of an oil spill or other source of heavy local mortality, such populations would be expected to increase back to approximately the same population level as prevailed before the losses. In order to incorporate such a response in the model, we need to determine what parameters are likely to change, and the possible magnitude of such changes. Our best current understanding of population dynamics suggests that survival of immatures is likely to increase after a substantial decrease in abundance, supposing food supplies are abundant.

Some evidence as to the possible upper limits of growth of sea otter populations in Alaska is available in data reported by Pitcher (1987). Since the results reported by Pitcher (1987) pertain to otters released in new areas, where food supplies are abundant and previously unexploited by sea otters, it is unlikely that the rates observed can realistically be used in the immediate aftermath of a reduction in numbers of a population presumably in equilibrium with its food supply. This is because it will take a number of years for the food supply to build up to the levels probably encountered by the newly released populations. The results do, however, suggest upper limits to population growth rates for use in selecting values of parameters to use in such circumstances (cf. Sec. 10.6).

The data considered here pertains to four locations in Southeast Alaska at which sea otters were released from 1965 to 1969. A number of surveys of the areas were conducted in subsequent years, under varying conditions, largely based on counts from small boats and by shoreline observers. Details of releases, locations, counts and survey conditions were reported by Pitcher (1987). A rough map of locations and a summary of the counts appears in Fig. 10.7. One small population (Necker Islands, south of Sitka) is not considered here.

Releases in the area north of Sitka were made in 1965, 1966, 1968 and 1969, but were grouped here at roughly the weighted average date (1968) with the weights being sizes of the individual releases). Data used here (Fig. 10.7) are those reported by Pitcher (1987:Tables 1 and 2). The first figure given is the number released, except for the Coronation Islands area, where otters evidently moved in from one of the other release sites. As often seems to be the case, newly released populations failed to grow rapidly (area north of Sitka) or actually decreased in the years following releases (Barrier and Maurelle Islands). Consequently, the regression calculations are all based on 1975 as a starting date.

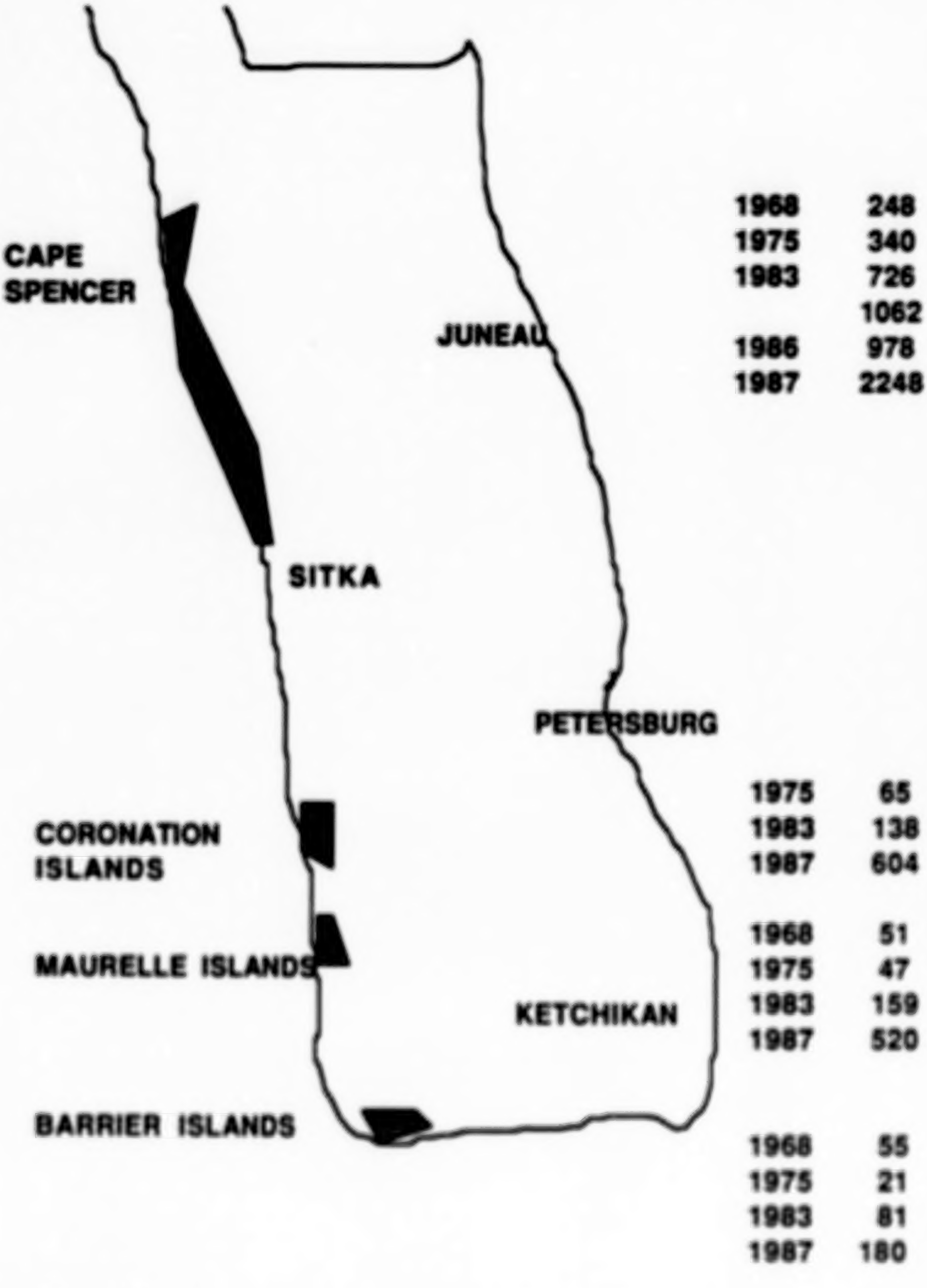


Fig. 10.7 Approximate locations of sea otter transplants in Southeastern Alaska with corresponding population estimates.

Fig. 10.8 shows regression plots of the natural logarithms of population size for the area north of Sitka and the Coronation Islands, while Fig. 10.9 shows the Barrier and Maurelle Islands data. Population growth rates for the area north of Sitka may be a little lower than those in the other areas, where annual rates appear to range from 18 to 20% per year. Annual rates of increase can be calculated from year to year, but these vary considerably, no doubt due to the fact that the fraction of otters present that were actually counted varied from year to year. We thus need to use some kind of averaging process with the count data, which are here considered to be indices or measures of relative abundance, rather than absolute estimates of the numbers present. Consequently, linear regressions are used on the logarithms of the set of counts for each area. Since it is unlikely that all otters present are actually counted, an estimate based on the current count and the number released will necessarily be an underestimate of the actual rate of increase, because the number released is an absolute value, while the current count presumably underestimates the number present.

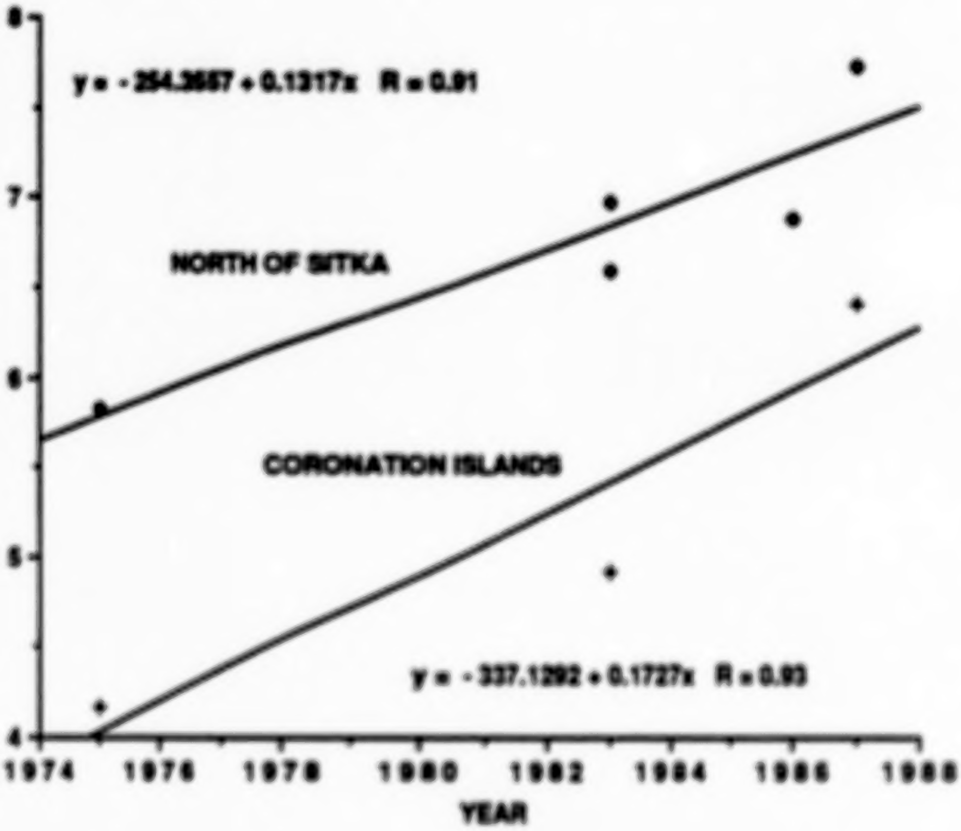


Fig. 10.8. Regression lines fitted to logarithms of sea otter counts for area north of Sitka (Fig. 10.7) and counts of otters in the Coronation Islands area. Slopes of regression lines approximate logarithms of finite rates of increase.

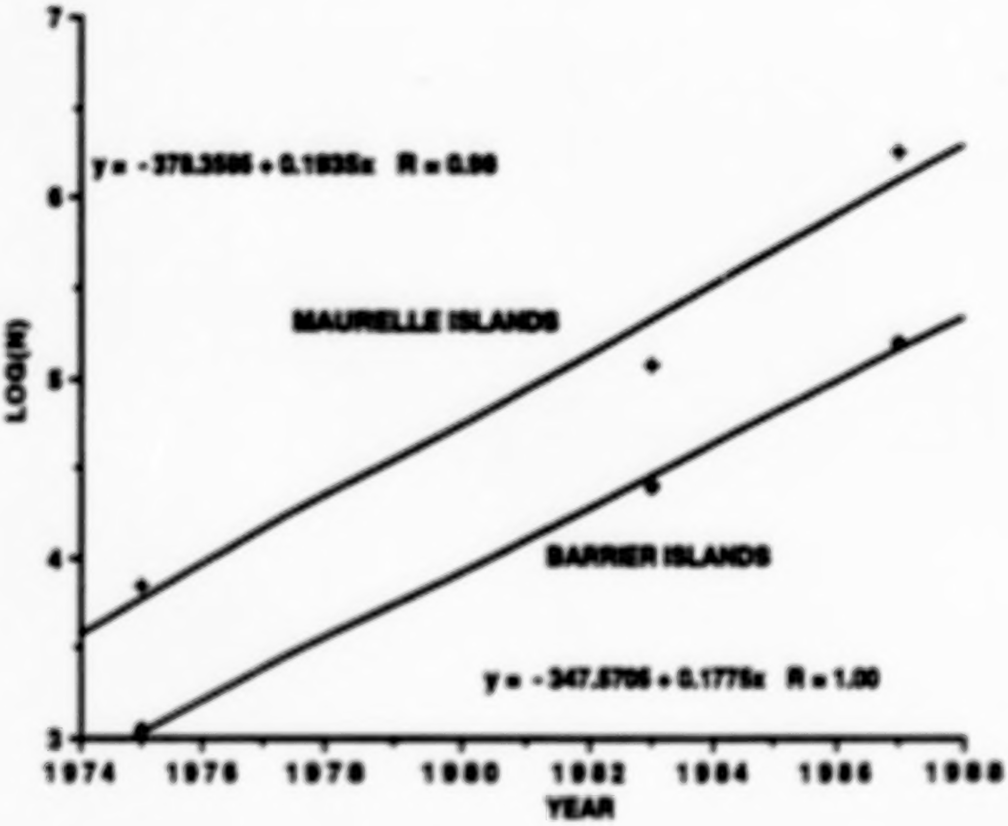


Fig. 10.9. Regressions on natural logarithms of counts of sea otters in the Maurelle and Barrier Islands areas.

10.6 Parameters for high population growth rates

The relatively high population growth rates observed in southeastern Alaska make it desirable to reassess parameter estimates considered earlier. One immediate conclusion is that the senescence curve of Fig. 7.3 is unlikely to support the higher growth curves, and thus needs to be replaced with that of Fig. 7.6, so that adult survivorship remains high out to about age 12. With this change (D= 0.305×10^{-6}, E= 1), increasing adult survivorship to 0.98, assuming survival to age 1 is 90% (F=0.0852), and 90% of fully adult females reproduce each year (A=0.45) gives a rate of increase of about 15% per year from the spreadsheet program (OTTERS) of Sec. 9.5 (Table 11.1). To achieve a rate of increase of 20% per year, it becomes necessary to assume that most adult females (about 80%) reproduce at age 3, rather than age 4 as previously assumed.

Various other combinations of values of the basic parameters might serve to achieve relatively high growth rates, but we have no data on which to base a choice of a particular set. However, it does appear evident that both early and adult survival must be very high, along with reproductive rates, and even so, annual population growth rates of 20% are not achieved unles extensive reproduction begins at age 3.

10.7 Likely parameter values for modelling the Alaska Peninsula population

In the absence of extensive biological data on the population of concern here, there is no reliable way to arrive at an appropriate selection of parameters. However, a general impression is that the population may have been relatively constant for a substantial period of time. One may then assume an approximate equilibrium with the food base, and it seems likely that parameters on the order of those observed for the California population may be assumed. Since there is evidence that the California population has been subject to a significant and probably relatively non-selective mortality from fishing nets, it may well be that adult survival is somewhat higher in the Alaska Peninsula area. But it is also true that there may be other forces leading to increased adult mortalities in that area, too.

In the aftermath of an oil spill, we can assume that early survival rates will increase in response to increases in food suppy associated with lowered sea otter population density. However, it seems unlikely that food conditions will approach those in the the newly invaded areas of Southeast Alaska unless otters remain absent for many years. Hence a realistic choice of parameters may be one based on modest improvements over rates observed in California. Adult survival in the range of 92-95% might thus be assumed, with annual reproductive rates of about 90%, and survival to age 1 on the order of 70-80%. Corresponding annual rates of increase then may be on the order of 5-10% per year.

11.0 APPENDIX

11.1 IBM-Compatible version of main models

This section of the report provides some notes on implementing the main model in LOTUS 1-2-3 on an IBM-compatible microcomputer. The programs used are essentially those described in the report and listed in Sec. 11.9, but converted to LOTUS formats. Two of the programs listed there (OTTERS and OTTERS4) and discussed in Sec. 9 provide the basis for the LOTUS version. In the work described in this report, the MULTIPLAN spreadsheet titled "OTTERS" served to estimate a rate of increase (λ) and stable age distribution which were then passed directly to the main program (OTTERS4) that contains all of the detail on the simulated population.

Since LOTUS does not permit "linked" spreadsheets, some minor changes have been necessary for the IBM-compatible version. The initial program (OTTERS) now serves only to estimate λ (identified as LMBD in the programs). The resulting value is then typed (via the computer keyboard) into OTTERS4, which now generates the stable age distribution used to prepare the initial population, and supplies all other details of the simulation without further entries, once the desired population parameters have been entered in the appropriate places.

In order to use the progams, it will be necessary to make appropriate choices of rates and parameters, after reviewing the present report. Since new data on Alaskan sea otters are continually being obtained, we strongly recommend that MMS staff discuss their approach with personnel of the Alaska Department of Fish and Game (Karl Schneider and Kenneth Pitcher) and of the U.S. Fish and Wildlife Service (Charles Monnett and A. DeGange) to take advantage of any new knowledge and local experience before implementing the spreadsheets needed for any future developments in the areas of concern here.

Seven parameters need to be supplied in both OTTERS and OTTERS4. The latter program also requires a list of assumed survival rates from a simulated oil spill at the far right of the spreadsheet. Structure of the spreadsheet is straight-forward, with few complications. Operation of various features of LOTUS 1-2-3 (printing, graphing, etc.) does require assistance from someone with a fair bit of experience with LOTUS, especially if any modifications of the program need to be made to suit new developments or requirements. For convenience in use of the program, a brief listing of references to sources in the main report follows.

The upper half of the main spreadsheet (OTTERS4) lists the female population and the lower half the males. The first 3 parameters (upper left corner) deal with reproduction. As noted in Sec. 9.3, the age of first reproduction (CAGE) was set as 3, corresponding to pregnancy initiated at about 42 months of age, with first births at about 48 months of age (age 0 refers to recruits to the population at the free-swimming stage at 6 months of chronological age, so that age-class 1 individuals are 18 months of age by the calendar). Present knowledge of sea otter population dynamics suggests leaving this parameter at 3, unless one wishes to simulate the high growth rates of Southeast Alaska (Sec. 10.5 and 10.6), where it would likely need to be changed to 2.

The second reproductive parameter (B) controls the rate of increase of the reproductive curve (Fig. 9.1) and is a largely arbitrary choice that probably cannot be checked until a great deal more data on ages at first pregnancy become available. The third reproductive parameter (A) controls the maximum rate of reproduction, set here as 0.30. As discussed in Sec. 8, it now appears that about 80-90% of fully mature female sea otters produce pups each year, about half of which are females. Since the model uses "recruits" individual otters at 6 months of age, the rate of birth of female young (0.4 to 0.45) has to be multiplied by survival from birth to 6 months of age, which is on the order of 0.5 to 0.6 (Sec. 7.6, 9.3). Consequently, the available data place the reproductive parameter (A) in a range of about 0.2 to 0.3. Due to the need to incorporate density-dependence in the final model (Sec. 9.8), we set A=0.30, thus yielding an annual rate of increase of about 4% (λ=1.04).

The next set of parameters to be considered (F,D,E,S1, and S) appear just above the l_x (survivorship) column for males at the lower left side of the spreadsheet. Two of these (D and E) control senescence and affect both reproduction and survival, thus controlling shape of the right side of the l_x and m_x curves (Fig. 9.1). As discussed in Sec. 7, the only data for estimating these rates comes from Schneider's (1976) sample in the Aleutians, which gives estimates that fit the data very well (Fig. 7.6), assuming an adult female survival rate of 0.982. As discussed in Sec. 9.3, we believe that it might be preferable to use the rather more arbitrary values given there that do not diminish survivorship so rapidly.

The other parameters control survival rates. The only estimate of early survival (F) comes from the California age structure data and is discussed in Sec. 7.4. This rate applies from weaning to some indefinite point when otters achieve the adult survival rates (S for females, S1 for males). Since so little is known about survivorship in this period, we have assumed the adult rate applies at 18 months of age (age class 1) and the major extra losses of the early period apply in the year after weaning (as seems evident in the field).

The only available information on male survivorship (S1) comes from the California age structure data. Rather than arbitrarily apply that rate in Alaska, we recommend assuming that the ratio of male and female survival rates observed there be used, as discussed in Sec. 9.3.

The remaining parameters (K and Z) that need to be specified for the model concern density-dependence, and are discussed in Sec. 9.8. We suggest maintaining the value of Z (11) presently employed, but note that the somewhat more conservative values (Fig. 9.4) might be tested in various applications of the model (these are more conservative in the sense that a reduced population will recover more slowly if lower values of Z are used). The parameter K denotes an asymptotic population size, which we arbitrarily set at 20,000 sea otters, so that the total realized population is on the order of 17,000 as estimated by Schneider (1976). In practice, MMS staff will no doubt want to develop spreadsheet models for various subregions of the Planning Areas.

When the data collected by Bruggeman (1987) become available in full detail, and decisions have been reached as to specific oil spill scenarios, it will be possible to consider likely seasonal patterns of abundance. That is, the present draft report (Bruggeman 1987) provides estimates of the total number of sea otters for entire Planning Areas. The main information on spatial distribution of these populations comes as "dot maps" (e.g., Bruggeman 1987:Fig. 6). Presumably this distributional data can be used to roughly allocate overall populations to those subregions of the Planning Areas for which spreadsheet models are needed. Runs of the models with "stationary" (constant) populations (and no oil spill mortality) can then be used to arrive at values of asymptotic populations (K) for each spreadsheet.

In our experience, the only satisfactory approach to modelling the populations is one of trial and error, aided by general knowledge of sea otter population dynamics (summarized in this report) and such current knowledge of Alaskan conditions as can be obtained. Possibly the iteritive process may also be facilitated by use of the BASIC model ("UNIMAK") of Sec. 11.3, if someone familiar with BASIC language is available to help out. In any case, the main effort will likely come from manipulation of the main spreadsheet (OTTERS4) as described above. Unless some more detailed biological information on the Planning Areas becomes available, we recommend determining all parameters other than K from work with a single implementation of the spreadsheet, after which values of K for subregions should be devised as suggested above (from the data of Bruggeman 1987).

If the BASIC program (UNIMAK) is utilized, it will supply an estimate of λ for any selected set of parameter estimates. Otherwise, a few minutes of iteration of the spreadsheet "OTTERS" is required to obtain the needed value for introduction as LMBD in the main program. This program (OTTERS) implements eq. (9.1) of Sec. 9.1. Once the selected parameter estimates (A,B,CAGE, D,E,F and S) have been introduced, all that is required is to try various values of LMBD until the quantity just to the right is nearly unity (this is the sum of the fourth column on the spreadsheet which sums the components of eq.(9.1), with $\lambda = e^{r}$). The simplest procedure is to start with LMBD = 1 and vary it until successive values of the quantity on the right bracket unity, and then make progressively smaller changes until it is within, say, 0.0001 or 0.00001 of unity. One then introduces LMBD in OTTERS4, and proceeds with that spreadsheet. The stable age structure (CX), reproductive rate (MX), survivorship (LX) and survival (SX) columns at the top left of OTTERS4 will agree with those in OTTERS, if the parameters all correspond in the two spreadsheets.

If a combination of rates is used that gives a stable age distribution concentrated in the younger age classes (e.g., rates of the type that must apply in Southeast Alaska to yield λ on the order of 1.2), it is possible that numbers smaller than the lower limit utilized by the program (or microcomputer) may be obtained in the older age classes (beyond 18 or 20). In this case, error messages may appear in many of the cells on the spreadsheet. In some spreadsheet programs (such as EXCEL) this can be avoided by setting a precision limit for entries in cells. In any case, it can be eliminated by removing (clearing) the offending cells in the MX and LX columns.

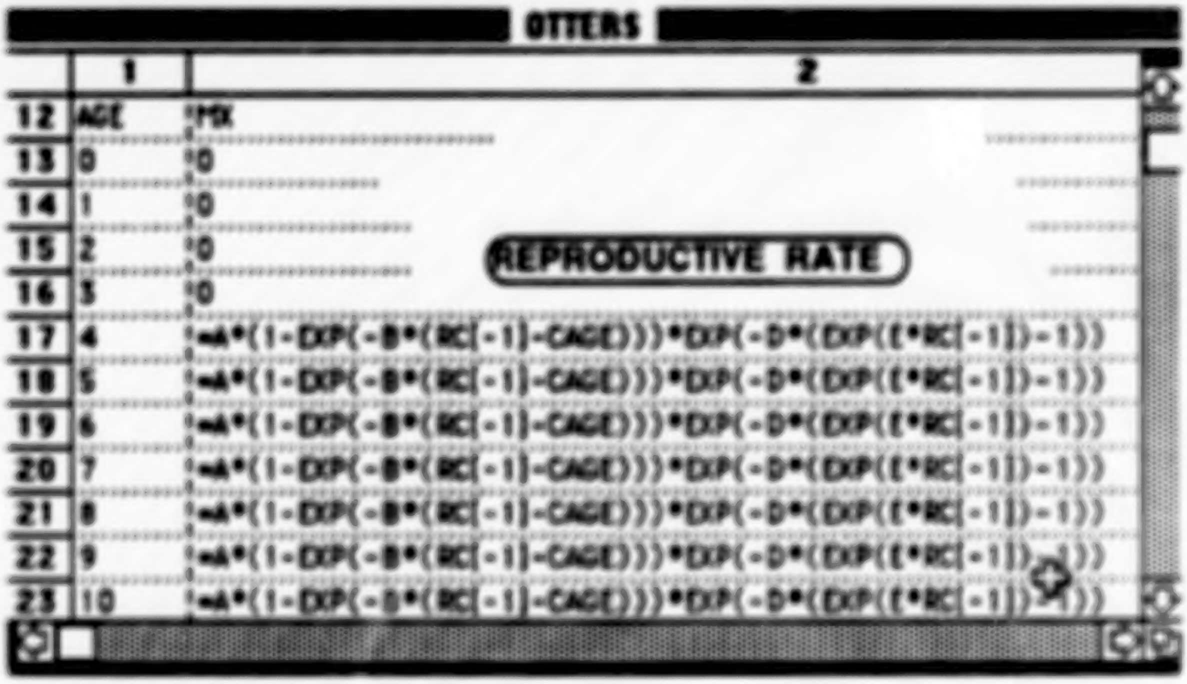
11.2 Formulas for MULTIPLAN MODELS

The following material briefly describes the formulas used in MULTIPLAN documents used to model sea otter populations in this report. In MULTIPLAN, each cell entry may be based on a formula of some sort. Hence the simple tabular output of a single spreadsheet may represent a fairly complex underlying model. The basic model of Table 11.1 (Section 11.9), titled "OTTERS" has a number of components, for which the underlying formulas can be displayed by a command in MULTIPLAN. The essential elements of these formulas are as follows.

Column 2 of the spreadsheet contains the m_x values for equation (9.4):

$$m_x = A[1 - e^{-B(x-C)}]\exp(-D(e^{Ex}-1)) \qquad (9.4)$$

The corresponding equation in the form used by MULTIPLAN is shown in the following section from a version of MULTIPLAN with the formulas displayed instead of the values calculated by the formulas. The entries designated by R[ ]C[ ] refer to rows and columns of the table with the entries in brackets designating the appropriate row and column, relative to the position of the given formula in the table. Thus RC[-1] denotes the entry in the same row, but one column before the present column, i.e., to the age entry in column 1.

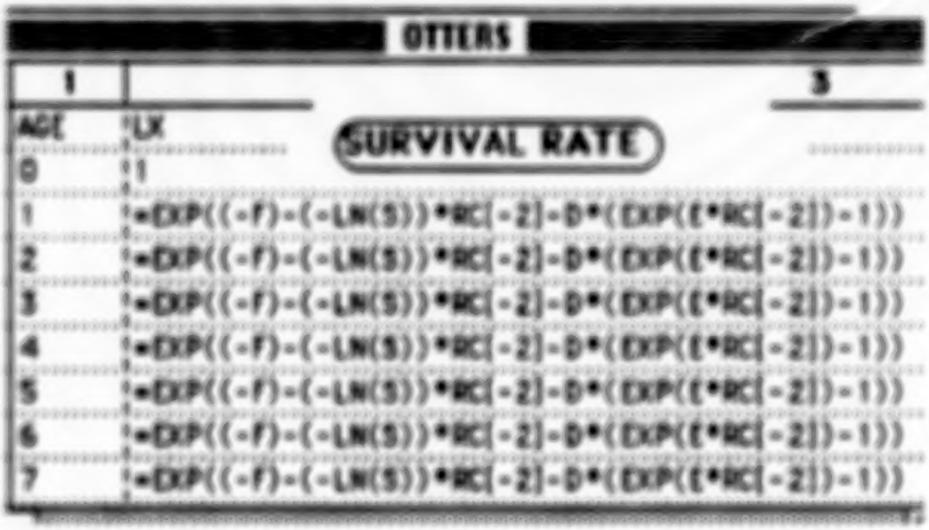


	1	2
12	AGE	MX
13	0	0
14	1	0
15	2	0
16	3	0
17	4	=A*(1-EXP(-B*(RC[-1]-CAGE)))*EXP(-D*(EXP(E*RC[-1])-1))
18	5	=A*(1-EXP(-B*(RC[-1]-CAGE)))*EXP(-D*(EXP(E*RC[-1])-1))
19	6	=A*(1-EXP(-B*(RC[-1]-CAGE)))*EXP(-D*(EXP(E*RC[-1])-1))
20	7	=A*(1-EXP(-B*(RC[-1]-CAGE)))*EXP(-D*(EXP(E*RC[-1])-1))
21	8	=A*(1-EXP(-B*(RC[-1]-CAGE)))*EXP(-D*(EXP(E*RC[-1])-1))
22	9	=A*(1-EXP(-B*(RC[-1]-CAGE)))*EXP(-D*(EXP(E*RC[-1])-1))
23	10	=A*(1-EXP(-B*(RC[-1]-CAGE)))*EXP(-D*(EXP(E*RC[-1])-1))

Survivorship was calculated from eq. (9.3):

$$l_x = \exp[-F - Gx - D(e^{Ex} - 1)] \tag{9.3}$$

and the corresponding entries from MULTIPLAN are:



1	3
AGE	LX
0	1
1	=EXP((-F)-(-LN(S))*RC[-2]-D*(EXP(E*RC[-2])-1))
2	=EXP((-F)-(-LN(S))*RC[-2]-D*(EXP(E*RC[-2])-1))
3	=EXP((-F)-(-LN(S))*RC[-2]-D*(EXP(E*RC[-2])-1))
4	=EXP((-F)-(-LN(S))*RC[-2]-D*(EXP(E*RC[-2])-1))
5	=EXP((-F)-(-LN(S))*RC[-2]-D*(EXP(E*RC[-2])-1))
6	=EXP((-F)-(-LN(S))*RC[-2]-D*(EXP(E*RC[-2])-1))
7	=EXP((-F)-(-LN(S))*RC[-2]-D*(EXP(E*RC[-2])-1))

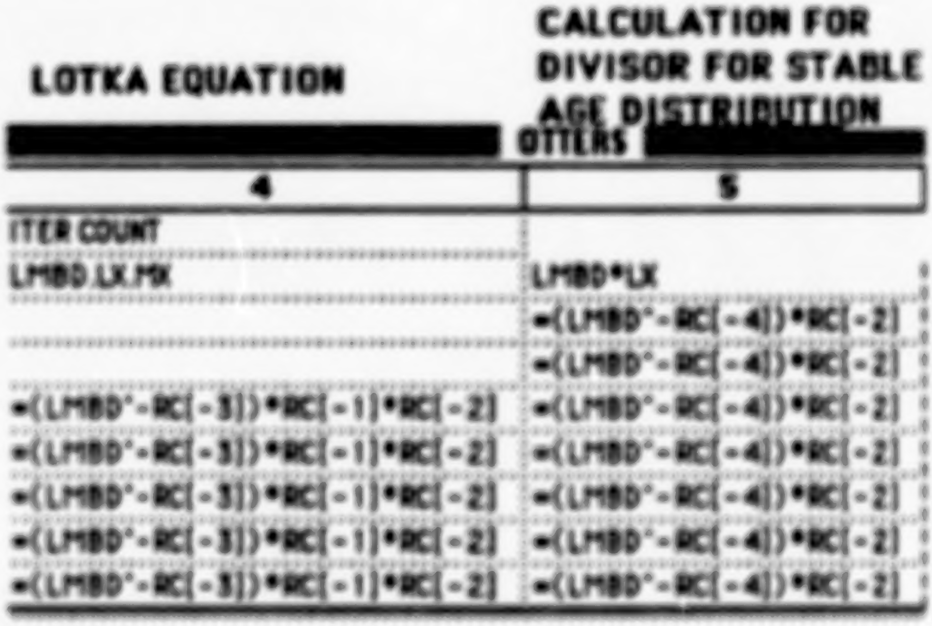
These two sets of values (l_x and m_x) are used to determine rate of increase from Lotka's equation:

$$1 = \sum_{a}^{w} e^{-rx} l_x m_x \qquad (9.1)$$

for which calculations are performed in the following portion of the MULTIPLAN table. In column 4 individual calculations are performed and then summed for equation (9.1), with LMBD=e^r. An iteritive solution is used to obtain a value of LMBD (described below) and the stable age distribution calculated from column 5, using the formula:

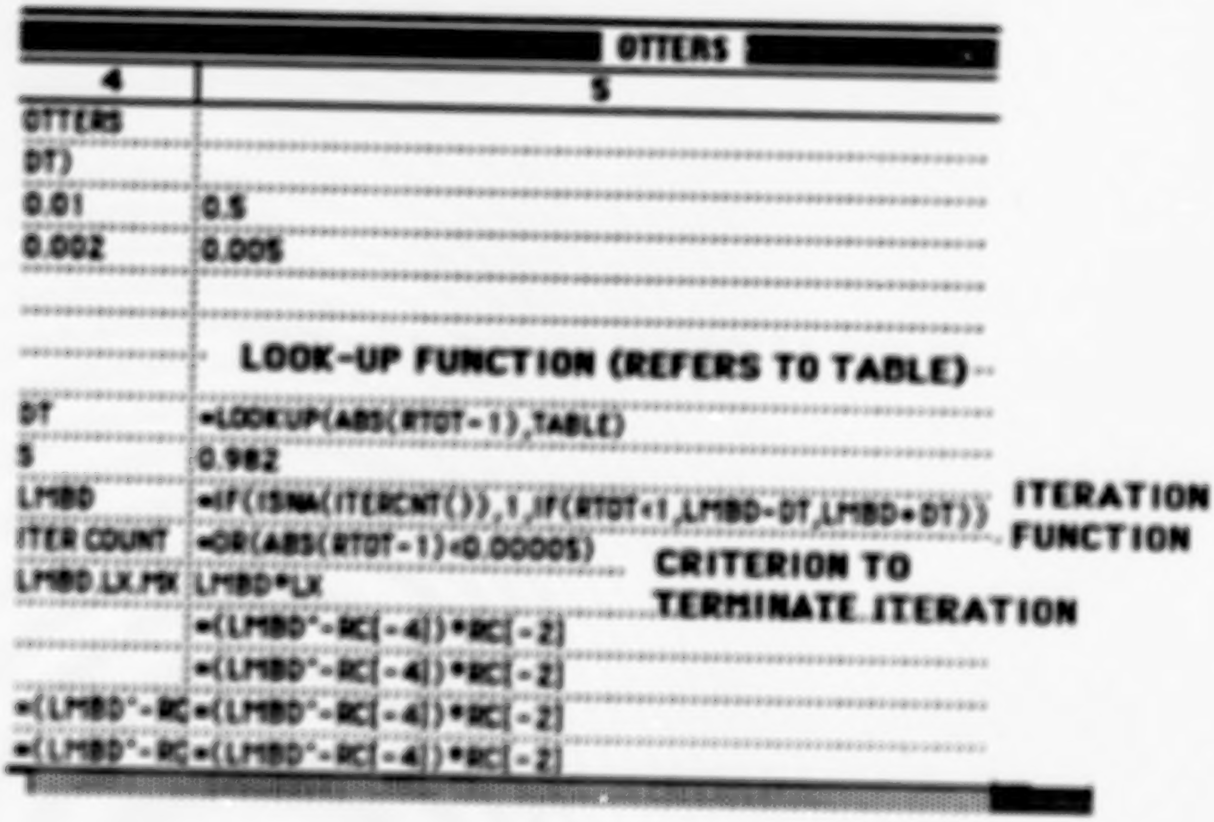
$$c_x = B\, e^{-rx} l_x \qquad (9.2)$$

Here, 1/B is the sum of the quantities in column 5, since c_x is a proportion (summing to unity). The values of c_x in column 6 of Table 11.1 are thus directly proportional to column 5.



LOTKA EQUATION	CALCULATION FOR DIVISOR FOR STABLE AGE DISTRIBUTION
	OTTERS
4	5
ITER COUNT	
LMBD.LX.MX	LMBD*LX
	=(LMBD^-RC[-4])*RC[-2]
	=(LMBD^-RC[-4])*RC[-2]
=(LMBD^-RC[-3])*RC[-1]*RC[-2]	=(LMBD^-RC[-4])*RC[-2]
=(LMBD^-RC[-3])*RC[-1]*RC[-2]	=(LMBD^-RC[-4])*RC[-2]
=(LMBD^-RC[-3])*RC[-1]*RC[-2]	=(LMBD^-RC[-4])*RC[-2]
=(LMBD^-RC[-3])*RC[-1]*RC[-2]	=(LMBD^-RC[-4])*RC[-2]
=(LMBD^-RC[-3])*RC[-1]*RC[-2]	=(LMBD^-RC[-4])*RC[-2]

The remaining calculations in the table produce the iteritive solution of Lotka's equation from the formula marked "iteration function" below.



OTTERS

4	5
OTTERS	
DT)	
0.01	0.5
0.002	0.005
DT	=LOOKUP(ABS(RTOT-1),TABLE)
S	0.982
LMBD	=IF((ISNA(ITERCNT()),1,IF(RTOT<1,LMBD-DT,LMBD+DT))
ITER COUNT	=OR(ABS(RTOT-1)<0.00005)
LMBD.LX.MX	LMBD*LX
	=((LMBD^-RC[-4])*RC[-2]
	=((LMBD^-RC[-4])*RC[-2]
=((LMBD^-RC	=((LMBD^-RC[-4])*RC[-2]
=((LMBD^-RC	=((LMBD^-RC[-4])*RC[-2]

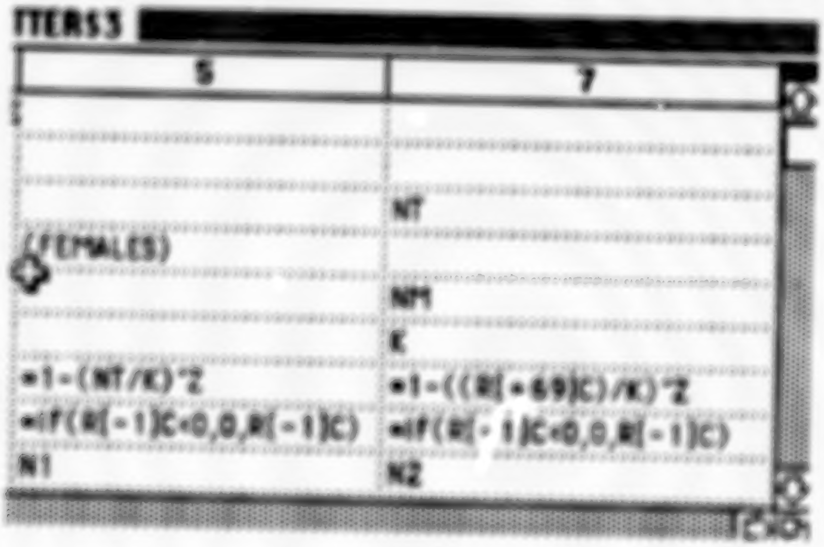
LOOK-UP FUNCTION (REFERS TO TABLE)

ITERATION FUNCTION

CRITERION TO TERMINATE ITERATION

This takes the sum of column 4 (RTOT) and increases or decreases it by DT until the sum is sufficiently close to unity (as determined by the criterion to terminate iteration in the line immediately below the iteration function). The increment, DT, is determined from the table at the top of the spreadsheet (Table 11.1) by the look-up function. This serves to speed up the iteration, and to permit a close approximation by reducing DT in stages as the total approaches unity.

One other feature of the MULTIPLAN details worth including here is that of the model used to control density dependence in OTTERS3 and OTTERS4:



TTERS3

5	7
	NT
(FEMALES)	
	NM
	K
=1-(NT/K)^Z	=1-((R[+69]C)/K)^Z
=IF(R[-1]C<0,0,R[-1]C)	=IF(R[-1]C<0,0,R[-1]C)
N1	N2

11.3 BASIC program (UNIMAK) corresponding to MULTIPLAN model

As indicated in Sec. 9.6, a projection model (OTTERS1) was used in development of the other models, and also serves to show the concurrence of the spreadsheet models with the BASIC program model intially developed as discussed in Sec. 9.2. The program is shown below.

The two programs give essentially the same results for the parameters used in OTTERS, yielding outputs as follows for an initial population of 17,170 otters (all considered to be females here):

OTTERS1	UNIMAK (BASIC program)
17172	17172
17175	17173
17178	17175
17181	17176
17183	17178
17186	17180
17187	17182
17188	17184
17189	17186
17191	17188

The small differences in the two sets of output are likely due to a slightly different approach to rounding off fractional individuals in the two programs.

UNIMAK -BASIC language program for sea otter projection model

```
10 REM POPULATION GROWTH WITH LESLIE MATRIX;
STARTING WITH STABLE AGE STRUCTURE AND CHANGING FIRST CLASS
20 REM ESTIMATES R FROM L(X)M(X) CURVE USING COMPOSITE CURVE
30 REM RUNS UNTIL STOPPED-- STORES TOTALS AND SQUARES
60 DIM V(50),L(50),M(50),C(50),N(50),R(50),Y(50)
80 REM PARAMETERS
90 REM ADULT REPRODUCTIVE RATE
100 A=.226
110 REM RATE OF APPROACH TO MAXIMUM REPRODUCTION
120 B=2
130 REM AGE OF FIRST REPRODUCTION
140 C=3
150 REM SENESCENCE
180 E=.2381
190 D=.04526
200 REM SURVIVAL RATES
210 G=-LOG(.982)
230 F=.0511
240 REM MAXIMUM AGE
250 W=25
260 L(0)=1
270 FOR X=1 TO W
280 L(X)=EXP(-F-G*X-D*(EXP(E*X)-1))
290 NEXT X
300 FOR X=C TO W
310 REM L(X)M(X) CURVE
320 M(X)=A*(1-EXP(-B*(X-C)))*EXP(-D*(EXP(E*X)-1))
```

```
330 Y(X)=L(X)*M(X)
340 NEXT X
350 FOR X=C TO W
360 R1=R1+EXP(-R*X)*Y(X)
370 NEXT X
380 REM TO LIMIT ITERATIONS
390 N1=N1+1
400 IF N1<200 THEN 440
410 PRINT"STUCK IN LOOP"
420 STOP
430 REM ITERATIVE SOLUTION
440 R2=ABS(R1-1)
450 D1=.01
460 IF R2<2 THEN D1=.005
470 IF R2<.1 THEN D1=.001
480 IF R2<.01 THEN D1=.0001
490 IF R2<.001 THEN D1=.00005
500 IF R2<.0005 THEN D1=.00001
510 IF R2<.0001 THEN 590
520 IF R1<1 THEN 560
530 R=R+D1
540 R1=0
550 GOTO 350
560 R=R-D1
570 R1=0
580 GOTO 350
590 PRINT "R=";R;"SUM=";R1
600 PRINT "S=";EXP(-G)
610 REM BIRTH RATE PER CAPITA
620 B1=0
630 FOR X=0 TO W
640 B1=B1+EXP(-R*X)*L(X)
650 NEXT X
660 B1=1/B1
670 REM AGE STRUCTURE
680 FOR X=0 TO W
690 C(X)=B1*EXP(-R*X)*L(X)
700 NEXT X
710 REM SAMPLE SIZE
720 N=17170
730 FOR X=0 TO W
740 N(X)=C(X)*N
750 N6=INT(N(X))
760 IF ABS(N6-N(X))>.5 THEN 790
770 N(X)=N6
780 GOTO 800
790 N(X)=N6+1
800 NEXT X
810 FOR X=0 TO W
820 N2=N2+N(X)
830 NEXT X
840 PRINT "SUM N(I)="N2
850 REM POPULATION PROJECTION
860 FOR X=1 TO W
870 L(X)=EXP(-F-G*X-D*(EXP(E*X)-1))
880 NEXT X
890 N3=1976
900 N3=N3+1
```

```
910 FOR X=0 TO W
920 R(X+1)=N(X)*L(X+1)/L(X)
930 NEXT X
940 FOR X=C TO W
950 R(0)=R(0)+R(X)*M(X)
960 NEXT X
970 FOR X=0 TO W
980 N4=INT(R(X))
990 IF ABS(N4-R(X))>.5 THEN 1020
1000 R(X)=N4
1010 GOTO 1030
1020 R(X)=N4+1
1030 N5=N5+R(X)
1040 N4=0
1050 NEXT X
1060 PRINT N3;" ";N5
1070 N5=0
1080 FOR X=0 TO W
1090 N(X)=R(X):R(X)=0
1100 NEXT X
1105 IF N3=1986 GOTO 1120
1110 GOTO 900
1120 STOP
```

11.4 BASIC program used to fit survivorship function to Aleutian age data

This program was used to find a minimum chi-square value for fits of the survivorship function (eq.(7.1)) to age structure data of female Aleutian sea otters, as described in Sec. 7.2. When a minimum chi-square was located, a minor modification of the program was used to print out observed and expected age structures, as shown in Fig. 7.3.

BASIC program "ALEUT1"

```
10 REM TO FIT L(X) CURVE TO
ALEUTIAN OTTER DATA
20 DIM C(30),O(30),L(30),E(30)
30 PRINT "T    S      CHI-SQ"
40 FOR S4=.97 TO .99 STEP .002
50 G=-LOG(S4)
60 C3=50
65 PRINT "S=";S4
70 REM OBSERVED AGE
FREQUENCIES
80  DATA  39,19,20,33,37,34,32,33,28
90  DATA  21,29,18,17,13,5,8,3,2,2
100 FOR I=0 TO 18
110 READ O(I)
120 NEXT I
150 FOR T=13 TO 15 STEP .2
160 FOR S=3 TO 5 STEP .2
170 REM SENESCENCE FUNCTION
180 E=1/S
190 D=EXP(-T/S)
220 L1=0
230 FOR X=4 TO 18
240 L(X)=EXP(-G*X-D*EXP(E*X)-1)
250 L1=L1+L(X)
270 NEXT X
300 FOR X=4 TO 18
310 C(X)=L(X)/L1
320 NEXT X
350 S2=0
360 FOR I=4 TO 18
380 S2=S2+O(I)
390 NEXT I
410 C2=0
420 REM CHI-SQUARE
430 FOR I=4 TO 18
440 E1=S2*C(I)
450 C1=((O(I)-E1)^2)/E1
460 C2=C2+C1
470 NEXT I
475 IF C2>=C3 GOTO 490
480 C3=C2:S3=S:T1=T
490 NEXT S
510 NEXT T
520 PRINT T1;"  ";S3;" ";C3
590 RESTORE
600 NEXT S4
```

11.5 BASIC program used to fit survivorship function to California age data

This program is very similar to that discussed in Sec. 11.4, except that the California sample represents ages of otters found dead, requiring a different formulation of the expected frequencies, as described in Sec. 7.3.

BASIC PROGRAM "CALIF"

```
10 REM TO FIT L(X) CURVE TO
CALIFORNIA OTTER DATA
20 DIM C(30),O(30),L(30),E(30)
30 PRINT "T    S      CHI-SQ"
40 FOR S4=.9 TO .92 STEP .002
50 G=-LOG(S4)
60 C3=50
65 PRINT "S=";S4
70 REM OBSERVED AGE
FREQUENCIES
80 DATA  28,31,13,17,20,18,11,18
90 DATA  8,14,5,9,1,2,1
100 FOR I=1 TO 15
110 READ O(I)
120 NEXT I
150 FOR T=10 TO 12 STEP .1
160 FOR S=2 TO 4 STEP .1
170 REM SENESCENCE FUNCTION
180 E=1/S
190 D=EXP(-T/S)
220 L2=0
230 FOR X=4 TO 16
240 L(X)=EXP(-G*X-D*EXP(E*X)-1)
250 L2=L2+O(X)
270 NEXT X
410 C2=0
420 REM CHI-SQUARE
430 FOR I=4 TO 15
440 E1=(L2/L(4))*(L(I)-L(I+1))
450 C1=((O(I)-E1)^2)/E1
460 C2=C2+C1
470 NEXT I
475 IF C2>=C3 GOTO 490
480 C3=C2:S3=S:T1=T
490 NEXT S
510 NEXT T
520 PRINT T1;"  ";S3;" ";C3
590 RESTORE
600 NEXT S4
```

11.6 BASIC program (ALEUT2) used to produce data for Fig. 7.6

The following program was used to produce data for plotting in Fig. 7.6. It also produces a chi-square table, for fit of data and model.

```
10 REM TO FIT L(X) CURVE TO
ALEUTIAN OTTER DATA
20 DIM C(30),O(30),L(30),E(30)
30 OPEN "CLIP:" FOR OUTPUT AS #1
40 S4=.915
50 G=-LOG(S4)
65 PRINT "S=";S4;
70 REM OBSERVED AGE
FREQUENCIES
80 DATA  39,19,20,33,37,34,32,33,28
90 DATA  21,29,18,17,13,5,8,3,2,2
100 FOR I=0 TO 18
110 READ O(I)
120 NEXT I
150 T=15
160 S=1
165 PRINT "T=";T;"S(T)=";S
170 REM SENESCENCE FUNCTION
180 E=1/S
190 D=EXP(-T/S)
220 L1=0
230 FOR X=4 TO 18
240 L(X)=EXP(-G*X-D*EXP(E*X)-1)
250 L1=L1+L(X)
270 NEXT X
300 FOR X=4 TO 18
310 C(X)=L(X)/L1
320 NEXT X
350 S2=0
360 FOR I=4 TO 18
380 S2=S2+O(I)
390 NEXT I
410 PRINT "AGE   OBSD    EXP
CHI-SQ"
420 REM CHI-SQUARE
430 FOR I=4 TO 18
440 E1=S2*C(I)
450 C1=((O(I)-E1)^2)/E1
460 PRINT I;" ";O(I);" ";
465 PRINT USING"##.###   ";E1;C1
470 WRITE #1,I,O(I),E1,C1
500 NEXT I
510 CLOSE #1
```

11.7 BASIC programs used to produce data for reproductive cycles. The first program (PWS REPRO CYCLE) generates data for Prince William Sound otters, and the second (CALIF REPRO CYCLE) produces data for "small" pups in California.

```
10 REM REPRODUCTIVE CYCLE
20 DIM Y(30),D(30),O(30)
30  DATA  .1,.22,.3,.41,.38,.33,.35
35  DATA  .16,.22,.05,0,0
40 FOR I=1 TO 18:D(I)=.01:NEXT I
50 FOR I=7 TO 18
60 READ O(I)
70 NEXT I
80 FOR I=1 TO 6:Y(I)=.05:NEXT I
90 FOR I=7 TO 10
100 D(I)=.1
110 NEXT I
120 LPRINT"MO.    ESTD   OBS
INCR"
130 FOR I=7 TO 18
140 Y(I)=Y(I-1)+D(I)-D(I-6)
150 SS=SS+((Y(I)-O(I))^2)
160 LPRINT USING "##     ";I;
170 LPRINT USING ".###
";Y(I);O(I);D(I)
180 NEXT I
185 LPRINT
190 LPRINT "SS=";SS
```

```
10 REM REPRODUCTIVE CYCLE
20 DIM Y(15),D(15),O(15)
30 DATA
.051,.096,.106,.113,.107,.1,.085,.043
35  DATA  .045,.082,.062,.066
40 FOR I=1 TO 15:D(I)=.0167:NEXT I
50 FOR I=4 TO 15
60 READ O(I)
70 NEXT I
80 Y(1)=.05:Y(2)=.05:Y(3)=.05
90 FOR I=4 TO 8
100 D(I)=.037
110 NEXT I
120 LPRINT"MO.   ESTD   OBSD
INCR"
130 FOR I=4 TO 15
140 Y(I)=Y(I-1)+D(I)-D(I-3)
150 SS=SS+((Y(I)-O(I))^2)
160 LPRINT USING "##  ";I;
170 LPRINT USING " .###
";Y(I);O(I);D(I)
180 NEXT I
190 LPRINT
200 LPRINT "SS=";SS
```

11.8 Bootstrap programs

The following programs were used in bootstrap calculations.

BOOT Adult female survival from telemetry data.

```
10 REM BOOTSTRAP FOR OTTER
SURVIVAL
20 DIM A(2,20),S(20)
25 OPEN "AFSURV" FOR OUTPUT AS
#1
30 REM ADULT FEMALES-
CALIFORNIA
40  DATA  1,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0
50 DATA
3,28,31,355,392,544,555,585,587
60 DATA 608,609,621,630,631,637,744
70 FOR I=1 TO 2:FOR J=1 TO 16
80 READ A(I,J)
90 NEXT J:NEXT I
100 REM BOOTSTRAP
102 RANDOMIZE TIMER
105 FOR I=1 TO 300' LOOP
110 K=0:S1=0:N1=0
120 Y=RND
130 Y=CINT(18*Y)
140 IF Y>16 GOTO 120
145 IF Y=0 GOTO 120
150 K=K+1
160 S1=S1+A(1,Y)
170 N1=N1+A(2,Y)
180 IF K<16 GOTO 120
190 S2=(1-(S1/N1))^365
200 PRINT S2
210 WRITE #1,S2
220 S=S+S2
230 S3=S3+S2^2
240 K1=K1+1
250 NEXT I ' END LOOP
260 S4=S/K1
270 S5=S3-(S^2)/K1
275 S5=S5/(K1-1)
280 PRINT "MEAN=";S4
290 PRINT "VARIANCE=";S5
300 PRINT "TOTAL=";K1
310 CLOSE #1
```

BOOT1 Program to calculate adult female survival from age data (ages 4-12).

```
10 REM BOOTSTRAP FOR AGE DATA
```

```
20 REM CALIFORNIA FEMALES AGES
4-12
30 DIM A(20),N(20)
40 REM CUMULATIVE AGES
50 DATA
0,17,37,55,66,84,92,106,111,120
60 FOR I=1 TO 10
70 READ A(I)
80 NEXT I
85 OPEN "AFSURVAGE" FOR
OUTPUT AS #1
90 RANDOMIZE TIMER
100 LPRINT TIME$
105 FOR I=1 TO 10 ' LOOP
110 FOR I1=1 TO 9:N(I1)=0:NEXT I1
120 K1=0:N=0:T=0:N2=0
130 Y=RND
140 Y=CINT(122*Y)
145 IF Y=0 GOTO 130
150 IF Y>120 GOTO 130
160 FOR J=1 TO 9
170 IF (Y>A(J) AND Y<=A(J+1)) THEN
N(J)=N(J)+1
175 NEXT J
180 K1=K1+1
190 IF K1<120 GOTO 130
200 REM SOLN OF EQN
202 FOR J=1 TO 9
204 N=N+N(J)
206 T=T+(J-1)*N(J)
208 NEXT J
210 S=.5
220 X=T/N
225 K=8'NO. OF AGES
230 REM GOTO ENDS HERE
240 X1=(S/(1-S))-(K+1)*((S^(K+1))/(1-
(S^(K+1))))
250 N2=N2+1:IF N2>2000 GOTO 510
260 R2=ABS(X-X1)
270 D=.04
280 IF R2<2 THEN D=.03
285 IF R2<1 THEN D=.01
290 IF R2<.1 THEN D=.001
300 IF R2<.01 THEN D=.0001
310 IF R2<.001 THEN D=.00001
320 IF R2<.0001 THEN 390
330 R1=X-X1
340 IF R1<0 THEN 370
350 S=S+D
360 GOTO 230
370 S=S-D
380 GOTO 230
390 PRINT "S=";S
395 WRITE #1,S
400 S1=S1+S
405 S2=S2+S^2
410 T1=T1+1
500 GOTO 560
510 LPRINT"STUCK IN LOOP"
520 FOR J=1 TO 9
530 LPRINT J+3;" ";N(J);" ";A(J+1)-A(J)
540 NEXT J
560 NEXT I ' END LOOP
570 S3=S1/T1
580 S4=S2-(S1^2/T1)
590 S4=S4/(T1-1)
595 LPRINT "BOOTSTRAP ON
CALFORNIA FEMALE AGES"
600 LPRINT "MEAN=";S3
610 LPRINT "VARIANCE=";S4
620 LPRINT "TOTAL=";T1
630 LPRINT TIME$
640 CLOSE #1
```

BOOT2 Program to calculate early survival from female age structure data (uses survival estimate obtained from age structure data, ages 4-12, also).

```
10 REM BOOTSTRAP FOR AGE DATA
20 REM CALIFORNIA FEMALES AGES
4-12
25 REM IST PART SAME AS BOOT1
(TO LINE 570)
30 DIM A(20),N(20)
40 REM CUMULATIVE AGES
50 DATA 0,28,59,72,89,109,127,138
55 DATA 156,164,178,183,192
60 FOR I=1 TO 13
70 READ A(I)
80 NEXT I
85 OPEN "LMDATA" FOR OUTPUT AS
#1
90 RANDOMIZE TIMER
100 PRINT TIME$
105 FOR I=1 TO 10 ' LOOP
110 FOR I1=1 TO 12:N(I1)=0:NEXT I1
120 K1=0:N=0:T=0:N2=0:N3=0:N4=0
130 Y=RND
140 Y=CINT(194*Y)
145 IF Y=0 GOTO 130
150 IF Y>192 GOTO 130
160 FOR J=1 TO 12
170 IF (Y>A(J) AND Y<=A(J+1)) THEN
N(J)=N(J)+1
175 NEXT J
180 K1=K1+1
190 IF K1<192 GOTO 130
```

```
200 REM SOLN OF EQN
202 FOR J=4 TO 12
204 N=N+N(J)
206 T=T+(J-4)*N(J)
208 NEXT J
210 S=.5
220 X=T/N
225 K=8'NO. OF AGES
230 REM GOTO ENDS HERE
240 X1=(S/(1-S))-(K+1)*((S^(K+1))/(1-
(S^(K+1))))
250 N2=N2+1:IF N2>2000 GOTO 510
260 R2=ABS(X-X1)
270 D=.04
280 IF R2<2 THEN D=.03
285 IF R2<1 THEN D=.01
290 IF R2<.1 THEN D=.001
300 IF R2<.01 THEN D=.0001
310 IF R2<.001 THEN D=.00001
320 IF R2<.0001 THEN 390
330 R1=X-X1
340 IF R1<0 THEN 370
350 S=S+D
360 GOTO 230
370 S=S-D
380 GOTO 230
390 PRINT "S,S0=";S;
400 S1=S1+S
405 S2=S2+S^2
410 T1=T1+1
500 GOTO  570
510 PRINT"STUCK IN LOOP"
520 FOR J=4 TO 12
530 PRINT J;" ";N(J);" ";A(J+1)-A(J)
540 NEXT J
570 REM CONTINUATION
700 REM  SOLN FOR F
710 N3=N(1)+N(2)
720 P=N3/(N+N3)
730 S0=(1-P)/(S^2-P*(S^12))
900 PRINT S0
905 WRITE #1,S0
910 S5=S5+S0
920 S6=S6+S0^2
930 T2=T2+1
1000 NEXT I ' END LOOP
1570 S3=S1/T1
1580 S4=S2-(S1^2/T1)
1590 S4=S4/(T1-1)
1600 S7=S5/T2
1610 S8=S6-(S5^2/T2)
1620 S8=S8/(T2-1)
1630 PRINT "BOOTSTRAP ON
CALIFORNIA FEMALE AGES"
1640 PRINT "MEAN SURVIVAL=";S3
1650 PRINT "VARIANCE=";S4
1655 PRINT "TOTAL=";T1
1660 PRINT "MEAN S0=";S7
1670 PRINT "VARIANCE=";S8
1680 PRINT "TOTAL=";T2
1700 PRINT TIME$
1710 CLOSE #1
```

BOOT3 Calculations for reproductive interval.

```
10 REM BOOTSTRAP FOR CDFG
REPRODUCTIVE DATA
20 REM DATA FROM WENDELL ET
AL. CALIF F&G J 1984
30 DIM M(30),W(30)
35 OPEN "CDFGREP" FOR OUTPUT
AS #1
40 REM DATA ARE MEAN INTERVALS
AND WEIGHTS
50 REM WEIGHTS ARE
RECIPROCALS OF MAXIMUM-
MINIMUM
60 DATA
22.15,12.85,12.2,10.15,13.65,11.05,19.
4,19.95,15.8,12.2,13.4,13.2
70 DATA
23.4,18.25,16.3,11.1,13.7,16.3,19.6,12.
85,12.65,10.55,14.15,11,7.5,9.95
80 DATA
.233,.769,.278,.204,.073,.137,.714,.303
,.167,.556,.094,.098,.167,.13
90 DATA
.147,.5,.128,.062,.069,.149,.4,.141,.10
1,.111,.078,.27
100 FOR I=1 TO 26:READ M(I):NEXT I
110 FOR I=1 TO 26:READ W(I):NEXT I
120 RANDOMIZE TIMER
130 PRINT TIME$
140 FOR I=1 TO 300' LOOP
150 K=0:WM=0:WT=0
170 Y=RND
180 Y=CINT(28*Y)
190 IF Y=0 GOTO 170
200 IF Y>26 GOTO 170
210 K=K+1
220 WM=WM+W(Y)*M(Y)
230 WT=WT+W(Y)
240 IF K<26 GOTO 170
250 X=WM/WT'WEIGHTED MEAN
255 X=12/X ' EST'D ANNUAL
REPROD. RATE
```

```
260 X1=X1+X
265 X2=X2+X^2
270 K1=K1+1
280 PRINT X
285 WRITE #1,X
290 NEXT I'  END LOOP
300 X3=X1/K1
310 S=X2-(X1^2/K1)
320 S=S/(K1-1)
330 PRINT "REPRODUCTIVE RATE
FROM CDFG DATA"
340 PRINT "MEAN=";X3
350 PRINT "VARIANCE=";S
360 PRINT "TOTAL=";K1
370 PRINT TIME$
380 CLOSE #1
```

BOOT3A Calculations for reproductive interval based on 5 observations from telemetry data and 5 of comparable accuracy from Wendell et al. 1984.

```
10 REM BOOTSTRAP FOR
REPRODUCTIVE INTERVAL  DATA
20 REM DATA FROM WENDELL ET
AL. CALIF F&G J 1984
25 REM (5 OBSNS) AND SINIFF
&RALLS 1987 (5 OBSNS)
30 DIM M(30),W(30)
35 OPEN "INTERV" FOR OUTPUT AS
#1
40 REM DATA ARE MEAN INTERVALS
50 REM WEIGHTS ARE
RECIPROCALS OF MAXIMUM-
MINIMUM
60 DATA  13.44,20.0,11.67,13.69,10.29
70 DATA  12.85,19.4,12.2,11.1,12.65
100 FOR I=1 TO 10:READ M(I):NEXT I
120 RANDOMIZE TIMER
130 PRINT TIME$
140 FOR I=1 TO 300' LOOP
150 K=0:WM=0
170 Y=RND
180 Y=CINT(12*Y)
190 IF Y=0 GOTO 170
200 IF Y>10 GOTO 170
210 K=K+1
220 WM=WM+M(Y)
240 IF K<10 GOTO 170
250 X=WM/10
255 X=12/X ' EST'D ANNUAL
REPROD. RATE
260 X1=X1+X
265 X2=X2+X^2
270 K1=K1+1
280 PRINT X
285 WRITE #1,X
290 NEXT I'  END LOOP
300 X3=X1/K1
310 S=X2-(X1^2/K1)
320 S=S/(K1-1)
330 PRINT "REPRODUCTIVE RATE
FROM INTERVAL DATA"
340 PRINT "MEAN=";X3
350 PRINT "VARIANCE=";S
360 PRINT "TOTAL=";K1
370 PRINT TIME$
380 CLOSE #1
```

BOOT4 Calculations for juvenile survival based on combined male and female juveniles observed through telemetry.

```
10 REM BOOTSTRAP FOR JUV.
OTTER SURVIVAL
20 DIM A(2,20),S(20)
30 REM JUVENILES
35 OPEN "JSURV" FOR OUTPUT AS #1
40  DATA  1,1,1,0,0,0,0,0,0,0,1,0,0,0,0
50 DATA 41,193,329,459,488,519
60 DATA
557,569,570,570,482,498,569,637,660
70 FOR I=1 TO 2:FOR J=1 TO 15
80 READ A(I,J)
90 NEXT J:NEXT I
100 REM BOOTSTRAP
102 RANDOMIZE TIMER
104 PRINT TIME$
105 FOR I=1 TO 300 ' LOOP
110 K=0:S1=0:N1=0
120 Y=RND
130 Y=CINT(17*Y)
140 IF Y>15 GOTO 120
145 IF Y=0 GOTO 120
150 K=K+1
160 S1=S1+A(1,Y)
170 N1=N1+A(2,Y)
180 IF K<15 GOTO 120
190 S2=(1-(S1/N1))^365 ' SURVIVAL
ESTIMATE
200 PRINT S2
210 WRITE #1,S2
220 S=S+S2
230 S3=S3+S2^2
240 K1=K1+1
250 NEXT I ' END LOOP
260 S4=S/K1
270 S5=S3-(S^2)/K1
```

```
275 S5=S5/(K1-1)
280 PRINT "MEAN=";S4
290 PRINT "VARIANCE=";S5
300 PRINT "TOTAL=";K1
310 CLOSE #1
```

BOOT5 Calculations for pup survival based on telemetry data.

```
10 REM PUP SURVIVAL
20 DIM A(20)
25 OPEN "PUPS" FOR OUTPUT AS #1
30 FOR I=1 TO 9:A(I)=1:NEXT I
40 FOR I=10 TO 18:A(I)=0:NEXT I
50 RANDOMIZE TIMER
60 PRINT TIME$
70 FOR I=1 TO 300 ' LOOP
80 S=0:K=0
90 Y=RND
100 Y=CINT(20*Y)
110 IF Y=O GOTO 90
120 IF Y>18 GOTO 90
130 K=K+1
140 S=S+A(Y)
150 IF K<18 GOTO 90
160 PRINT S/18
165 WRITE #1,S/18
170 S1=S1+S/18
180 S2=S2+(S/18)^2
190 K1=K1+1
200 NEXT I
210 S3=S2-(S1^2/K1)
220 PRINT "BOOTSTRAP FOR PUP
SURIVIVAL"
230 PRINT "MEAN=";S1/K1
240 PRINT "OVERALL
VARIANCE=";S3/(K1-1)
245 PRINT "TOTAL=";K1
250 PRINT "BINOMIAL
VARIANCE=";(.5)^2/18
260 CLOSE #1
```

BOOT5A Calculations for pup survival based on marking data, using expanded sample.

```
10 REM PUP SURVIVAL
20 DIM A(200)
25 OPEN "PUPS" FOR OUTPUT AS #1
30 FOR I=1 TO 40:A(I)=1:NEXT I
40 FOR I=41 TO 72:A(I)=0:NEXT I
50 RANDOMIZE TIMER
60 PRINT TIME$
70 FOR I=1 TO 10 ' LOOP
80 S=0:K=0
90 Y=RND
100 Y=CINT(74*Y)
110 IF Y=O GOTO 90
120 IF Y>72 GOTO 90
130 K=K+1
140 S=S+A(Y)
150 IF K<72 GOTO 90
160 PRINT S/72
165 WRITE #1,S/72
170 S1=S1+S/72
180 S2=S2+(S/72)^2
190 K1=K1+1
200 NEXT I
210 S3=S2-(S1^2/K1)
220 PRINT "BOOTSTRAP FOR PUP
SURIVIVAL"
230 PRINT "MEAN=";S1/K1
240 PRINT "OVERALL
VARIANCE=";S3/(K1-1)
245 PRINT "TOTAL=";K1
250 PRINT "BINOMIAL
VARIANCE=";(.5)^2/72
260 CLOSE #1
```

BOOT6 Program to calculate bootstrap estimate for early survival, using data of Ames'.

```
10 REM EARLY SURVIVAL FROM
AMES' DATA
20 DIM A(800)
25 OPEN "LMDATA" FOR OUTPUT AS
#1
30 FOR I=1 TO 183:A(I)=1:NEXT I
40 FOR I=184 TO 708:A(I)=0:NEXT I
50 RANDOMIZE TIMER
60 PRINT TIME$
70 FOR I=1 TO 10 ' LOOP
80 S=0:K=0
90 Y=RND
100 Y=CINT(710*Y)
110 IF Y=O GOTO 90
120 IF Y>708 GOTO 90
130 K=K+1
140 S=S+A(Y)
150 IF K<708 GOTO 90
160 PRINT S/708
165 WRITE #1,S/708
170 S1=S1+S/708
180 S2=S2+(S/708)^2
190 K1=K1+1
200 NEXT I
210 S3=S2-(S1^2/K1)
220 PRINT "BOOTSTRAP FOR EARLY
SURVIVAL"
230 PRINT "MEAN=";S1/K1
```

```
240 PRINT "OVERALL
VARIANCE=";S3/(K1-1)
245 PRINT "TOTAL=";K1
250 PRINT "BINOMIAL
VARIANCE=";(.2585)^2/708
260 CLOSE #1
```

BOOTS. Program to estimate rate of change based on telemetry data.

```
10 REM BOOTSTRAP FOR RATE OF
CHANGE
30 DIM B(4,1000)
40 OPEN "PUPS" FOR INPUT AS #1
50 OPEN "JSURV" FOR INPUT AS #2
60 OPEN "AFSURV" FOR INPUT AS #3
70 OPEN "INTERV" FOR INPUT AS #4
75 OPEN "LOTKA" FOR OUTPUT AS
#5
80 N=10 ' NO. OF TRIALS
90 W=15 ' MAXIMUM AGE
100 A=4 : M=3 ' AGE 1ST REPROD.;
AGE MATURITY
110 FOR I=1 TO N
120 INPUT #1, B(1,I)
130 INPUT #2, B(2,I)
140 INPUT #3, B(3,I)
150 INPUT #4, B(4,I)
155 B(4,I)=B(4,I)/2
160 NEXT I
200 FOR I=1 TO N
203 N2=0
205 L=1.01
210 LM=B(1,I)*(B(2,I)^(M-.5)) '
SURVIVAL TO AGE 3
220 S=B(3,I) ' ADULT SURVIVAL
230 F=B(4,I) ' REPRODUCTIVE RATE
240 X1=1-((S/L)^(W-A+1))
250 X2=1-(S/L)
260 X=(L^(-A))*LM*(S^(A-
M))*F*(X1/X2)
270 N2=N2+1:IF N2>2000 GOTO 560
280 R2=ABS(X-1)
290 D=.04
300 IF R2<2 THEN D=.03
310 IF R2<1 THEN D=.01
320 IF R2<.1 THEN D=.001
330 IF R2<.01 THEN D=.0001
340 IF R2<.001 THEN D=.00001
350 IF R2<.0001 THEN 420
360 R1=X-1
370 IF R1<0 THEN 400
380 L=L+D
390 GOTO 260
400 L=L-D
410 GOTO 260
420 PRINT "LAMBDA=";L
425 WRITE #5,L
430 L1=L1+L
440 L2=L2+L^2
450 T1=T1+1
460 NEXT I ' END LOOP
470 PRINT "MEAN=";L1/T1
480 L3=L2-(L1^2)/T1
490 PRINT "VARIANCE=";L3/(T1-1)
500 PRINT "TOTAL=";T1
550 GOTO 570
560 PRINT "STUCK IN LOOP"
570 CLOSE #1:CLOSE#2:CLOSE
#3:CLOSE#4:CLOSE#5
```

BOOTS2. Program to calculate lambda using estimates of early survival from age data, etc.

```
10 REM BOOTSTRAP FOR RATE OF
CHANGE
30 DIM B(4,1000)
40 OPEN "LMDATA" FOR INPUT AS #1
50 OPEN "AFSURVAGE" FOR INPUT
AS #2
60 OPEN "CDFGREP" FOR INPUT AS
#3
65 OPEN "PUPS" FOR INPUT AS #4
75 OPEN "LOTKA" FOR OUTPUT AS
#5
80 N=10 ' NO. OF TRIALS
90 W=15 ' MAXIMUM AGE
100 A=4 : M=3 ' AGE 1ST REPROD.;
AGE MATURITY
110 FOR I=1 TO N
120 INPUT #1, B(1,I) '  EARLY
SURVIVAL
130 INPUT #2, B(2,I) ' ADULT
SURVIVAL
140 INPUT #3, B(3,I) '
REPRODUCTION
150 INPUT #4,B(4,I) ' PUP SURVIVAL
155 B(3,I)=B(3,I)/2
160 NEXT I
200 FOR I=1 TO N
203 N2=0
205 L=1.01
210 LM=B(1,I)*(B(2,I)^M) ' SURVIVAL
TO AGE 3
220 S=B(2,I) ' ADULT SURVIVAL
230 F=B(3,I)*B(4,I) ' REPRODUCTIVE
RATE
240 X1=1-((S/L)^(W-A+1))
250 X2=1-(S/L)
```

```
260 X=(L^(-A))*LM*(S^(A-
M))*F*(X1/X2)
270 N2=N2+1:IF N2>2000 GOTO 560
280 R2=ABS(X-1)
290 D=.04
300 IF R2<2 THEN D=.03
310 IF R2<1 THEN D=.01
320 IF R2<.1 THEN D=.001
330 IF R2<.01 THEN D=.0001
340 IF R2<.001 THEN D=.00001
350 IF R2<.0001 THEN 420
360 R1=X-1
370 IF R1<0 THEN 400
380 L=L+D
390 GOTO 260
400 L=L-D
410 GOTO 260
420 PRINT "LAMBDA=";L
425 WRITE #5,L
430 L1=L1+L
440 L2=L2+L^2
450 T1=T1+1
460 NEXT I ' END LOOP
470 PRINT "MEAN=";L1/T1
480 L3=L2-(L1^2)/T1
490 PRINT "VARIANCE=";L3/(T1-1)
500 PRINT "TOTAL=";T1
550 GOTO 570
560 PRINT "STUCK IN LOOP"
570 CLOSE #1:CLOSE#2:CLOSE
#3:CLOSE#4:CLOSE#5
```

BOOTS2A Revision for use with early survival based on Amys' data--changes at lines 170-190 from BOOTS2

```
10 REM BOOTSTRAP FOR RATE OF
CHANGE
30 DIM B(4,1000)
40 OPEN "LMDATA" FOR INPUT AS #1
50 OPEN "AFSURVAGE" FOR INPUT
AS #2
60 OPEN "CDFGREP" FOR INPUT AS
#3
65 OPEN "PUPS" FOR INPUT AS #4
75 OPEN "LOTKA" FOR OUTPUT AS
#5
80 N=10 ' NO. OF TRIALS
90 W=15 ' MAXIMUM AGE
100 A=4 : M=3 ' AGE 1ST REPROD.;
AGE MATURITY
110 FOR I=1 TO N
120 INPUT #1, B(1,I) '  PROPORTION
FROM BOOT6
130 INPUT #2, B(2,I) ' ADULT
SURVIVAL
140 INPUT #3, B(3,I) '
REPRODUCTION
150 INPUT #4,B(4,I) ' PUP SURVIVAL
155 B(3,I)=B(3,I)/2
160 NEXT I
165 REM CALCULATES S0
170 FOR I=1 TO N
180 B(1,I)=(1-B(1,I))/(B(2,I)^2)
190 NEXT I
200 FOR I=1 TO N
203 N2=0
205 L=1.01
210 LM=B(1,I)*(B(2,I)^M) ' SURVIVAL
TO AGE 3
220 S=B(2,I) ' ADULT SURVIVAL
230 F=B(3,I)*B(4,I) ' REPRODUCTIVE
RATE
240 X1=1-((S/L)^(W-A+1))
250 X2=1-(S/L)
260 X=(L^(-A))*LM*(S^(A-
M))*F*(X1/X2)
270 N2=N2+1:IF N2>2000 GOTO 560
280 R2=ABS(X-1)
290 D=.04
300 IF R2<2 THEN D=.03
310 IF R2<1 THEN D=.01
320 IF R2<.1 THEN D=.001
330 IF R2<.01 THEN D=.0001
340 IF R2<.001 THEN D=.00001
350 IF R2<.0001 THEN 420
360 R1=X-1
370 IF R1<0 THEN 400
380 L=L+D
390 GOTO 260
400 L=L-D
410 GOTO 260
420 PRINT "LAMBDA=";L
425 WRITE #5,L
430 L1=L1+L
440 L2=L2+L^2
450 T1=T1+1
460 NEXT I ' END LOOP
470 PRINT "MEAN=";L1/T1
480 L3=L2-(L1^2)/T1
490 PRINT "VARIANCE=";L3/(T1-1)
500 PRINT "TOTAL=";T1
550 GOTO 570
560 PRINT "STUCK IN LOOP"
570 CLOSE #1:CLOSE#2:CLOSE
#3:CLOSE#4:CLOSE#5
```

11.9 Outputs from MULTIPLAN spreadsheet models.

"OTTERS"

A list of the parameters is at the upper left side of the spreadsheet, with the exception of the adult survival rate (S), which is at the right. The table at the top provides values of "DT", used to make progressively smaller changes in the rate of increase as iterations proceed in solving the Lotka equation (eq.(9.1)). The rate of increase is "LMBD" ($\lambda = e^r$) and the entry just to the right of it is the sum of the terms in eq.(9.1), which is within a small range around unity, controlled by "ITER COUNT". The first 3 columns of the main body of the table contain ages, and the m_x and l_x curves given by eqs. (9.3) and (9.4). Column 4 contains the components of the Lotka equation (eq.(9.1)), summing to within a small increment of unity, as seen at the bottom of the column. Column 5 contains quantities needed for the stable age distribution given in column 6 (calculated from eq. (9.2)). The final column shows individual age-specific survival rates, calculated from column 3 as $s_x = l_{x+1}/l_x$. The various components of the table are computed by the appropriate equations as described in detail in Sec. 11.2. These equations can be displayed by an appropriate command in MULTIPLAN.

"OTTERS2"

The upper panel of the model contains the data on females. Columns 2-4 are linked to OTTERS and supply the essential components for projections: initial stable age distribution (c_x), survival rates (s_x) and reproductive rates (m_x). An initial population (N_T) at the top of the table is partitioned into females and males, as described in sec. 9.7. The initial population of females is distributed by age class according to the stable age distribution (c_x) and then projected forwards a year by using the survival rates (s_x) of column 5 to yield all but the first entry of column 6 (N1). The first entry of column 6 is generated by multiplying each subsequent entry by the age-specific reproductive rate(m_x) in column 2 (these products are in columns 6, 8, 10, etc. which are not shown in the output table, but can be made visible as needed). The subsequent age vectors (N2, N3, etc.) are generated in the same manner, except that the column entries after the first are produced from the entries in the previous column. The age vector of the initial population is not shown, since it is proportional to the stable age distribution of column 3.

Table 11.1 Example of output for sea otter model.

	1	2	3	4	5	6	7
1				OTTERS			
2		TABLE	(VALUES OF	DT)			
3	0	0.00001	0.00100	0.01000	0.50000	0.10000	1
4	0.000005	0.00001	0.00010	0.00200	0.00500	0.01000	0.10000
5	PARAMS						
6	F	0.05110					
7	A	0.23600					
8	B	2.00000		DT	0.00001		
9	CAGE	3.00000		S	0.98200		
10	D	0.04526		LMBD	1.00005	0.99998	
11	E	0.23810		ITER COUNT	TRUE		
12	AGE	MX	LX	LMBD LX MX	LMBD*LX	CX	SX
13	0	0.00000	1.00000		1.00000	0.09933	0.92180
14	1	0.00000	0.92180		0.92175	0.09156	0.96696
15	2	0.00000	0.89134	0.00000	0.89125	0.08853	0.96295
16	3	0.00000	0.85831	0.00000	0.85818	0.08524	0.95789
17	4	0.18183	0.82217	0.14946	0.82201	0.08165	0.95151
18	5	0.20003	0.78231	0.15644	0.78211	0.07769	0.94348
19	6	0.19528	0.73809	0.14408	0.73787	0.07329	0.93339
20	7	0.18601	0.68892	0.12810	0.68868	0.06841	0.92073
21	8	0.17446	0.63431	0.11061	0.63406	0.06298	0.90492
22	9	0.16077	0.57400	0.09223	0.57375	0.05699	0.88525
23	10	0.14483	0.50814	0.07360	0.50789	0.05045	0.86091
24	11	0.12706	0.43746	0.05555	0.43722	0.04343	0.83099
25	12	0.10752	0.36353	0.03906	0.36331	0.03609	0.79451
26	13	0.08699	0.28882	0.02511	0.28864	0.02867	0.75052
27	14	0.06649	0.21677	0.01440	0.21662	0.02152	0.69819
28	15	0.04727	0.15134	0.00715	0.15123	0.01502	0.63702
29	16	0.03066	0.09641	0.00295	0.09633	0.00957	0.56705
30	17	0.01771	0.05467	0.00097	0.05462	0.00543	0.48922
31	18	0.00882	0.02674	0.00024	0.02672	0.00265	0.40365
32	19	0.00364	0.01085	0.00004	0.01084	0.00108	0.31984
33	20	0.00119	0.00347	0.00000	0.00347	0.00034	0.23657
34	21	0.00029	0.00082	0.00000	0.00082	0.00008	0.16135
35	22	0.00005	0.00013	0.00000	0.00013	0.00001	0.09929
36	23	0.00000	0.00001	0.00000	0.00001	0.00000	0.05363
37	24	0.00000	0.00000	0.00000	0.00000	0.00000	0.02454
38	25	0.00000	0.00000	0.00000	0.00000	0.00000	#VALUE!
39			R	0.99998	SUMCX	1.00000	
40							
41							
42							
43							
44							
45							
46							
47							
48							
49							
50							
51							
52							

Table 11.3 Otter population model with A=0.30 to give increasing population.

	1	2	3	4	5	6	7
1				OTTERS			
2		TABLE	(VALUES OF	DT)			
3	0	0.00001	0.00100	0.01000	0.50000	0.10000	1
4	0.000005	0.00001	0.00010	0.00200	0.00500	0.01000	0.10000
5	PARAMS						
6	F	0.05110					
7	A	0.30000					
8	B	2.00000		DT	0.00001		
9	CAGE	3.00000		S	0.98200		
10	D	0.04526		LMBD	1.03998	0.99999	
11	E	0.23810		ITER COUNT	TRUE		
12	AGE	MX	LX	LMBD.LX.MX	LMBD*LX	CX	SX
13	0	0.00000	1.00000		1.00000	0.12299	0.92180
14	1	0.00000	0.92180		0.88636	0.10901	0.96696
15	2	0.00000	0.89134	0.00000	0.82412	0.10136	0.96295
16	3	0.00000	0.85831	0.00000	0.76308	0.09385	0.95789
17	4	0.24137	0.82217	0.16964	0.70285	0.08644	0.95151
18	5	0.26553	0.78231	0.17074	0.64306	0.07909	0.94348
19	6	0.25923	0.73809	0.15122	0.58339	0.07175	0.93339
20	7	0.24692	0.68892	0.12928	0.52360	0.06440	0.92073
21	8	0.23158	0.63431	0.10734	0.46356	0.05701	0.90492
22	9	0.21341	0.57400	0.08607	0.40336	0.04961	0.88525
23	10	0.19239	0.50814	0.06605	0.34335	0.04223	0.86091
24	11	0.16867	0.43746	0.04793	0.28423	0.03496	0.83099
25	12	0.14273	0.36353	0.03241	0.22711	0.02793	0.79451
26	13	0.11548	0.28882	0.02003	0.17350	0.02134	0.75052
27	14	0.08826	0.21677	0.01105	0.12521	0.01540	0.69819
28	15	0.06275	0.15134	0.00527	0.08406	0.01034	0.63702
29	16	0.04070	0.09641	0.00210	0.05149	0.00633	0.56705
30	17	0.02350	0.05467	0.00066	0.02807	0.00345	0.48922
31	18	0.01171	0.02674	0.00015	0.01321	0.00162	0.40565
32	19	0.00484	0.01085	0.00002	0.00515	0.00063	0.31984
33	20	0.00158	0.00347	0.00000	0.00158	0.00019	0.23657
34	21	0.00038	0.00082	0.00000	0.00036	0.00004	0.16135
35	22	0.00006	0.00013	0.00000	0.00006	0.00001	0.09929
36	23	0.00001	0.00001	0.00000	0.00001	0.00000	0.05363
37	24	0.00000	0.00000	0.00000	0.00000	0.00000	0.02454
38	25	0.00000	0.00000	0.00000	0.00000	0.00000	
39			R	0.99999	SUMCX	1.00000	
40							
41							
42							
43							
44							
45							
46							
47							
48							
49							
50							
51							
52							

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END

8—30—91